

# PERSISTENCE IN FLUCTUATING ENVIRONMENTS FOR INTERACTING STRUCTURED POPULATIONS

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**ABSTRACT.** Individuals within any species exhibit differences in size, developmental state, or spatial location. These differences coupled with environmental fluctuations in demographic rates can have subtle effects on population persistence and species coexistence. To understand these effects, we provide a general theory for coexistence of structured, interacting species living in a stochastic environment. The theory is applicable to nonlinear, multi species matrix models with stochastically varying parameters. The theory relies on long-term growth rates of species corresponding to the dominant Lyapunov exponents of random matrix products. Our coexistence criterion requires that a convex combination of these long-term growth rates is positive with probability one whenever one or more species are at low density. When this condition holds, the community is stochastically persistent: the fraction of time that a species density goes below  $\delta > 0$  approaches zero as  $\delta$  approaches zero. Applications to predator-prey interactions in an autocorrelated environment, a stochastic LPA model, and spatial lottery models are provided. These applications demonstrate that positive autocorrelations in temporal fluctuations can disrupt predator-prey coexistence, fluctuations in log-fecundity can facilitate persistence in structured populations, and long-lived, relatively sedentary competing populations are likely to coexist in spatially and temporally heterogenous environments.

## 1. INTRODUCTION

All populations are structured and experience environmental fluctuations. Population structure may arise to individual differences in age, size, and spatial location [Metz and Diekmann, 1986, Caswell, 2001, Holyoak et al., 2005]. Temporal fluctuations in environmental factors such light, precipitation, and temperature occur in all natural marine, freshwater and terrestrial systems. Since these environmental factors can influence survival, growth, and reproduction, environmental fluctuations result in demographic fluctuations that may influence species persistence and the composition of ecological communities [Tuljapurkar, 1990, Chesson, 2000b, Kuang and Chesson, 2009]. Here we present, for the first time, a general approach to studying coexistence of structured populations in fluctuating environments.

For species interacting in an ecosystem, a fundamental question is what are the minimal conditions to ensure the long-term persistence of all species. Historically, theoretical ecologists characterize persistence by the existence of an asymptotic equilibrium in which the proportion of each population is strictly positive [May, 1975, Roughgarden, 1979]. More recently, coexistence was equated with the existence of an attractor bounded away from extinction [Hastings, 1988], a definition that ensures populations will persist despite small, random perturbations of the populations [Schreiber, 2006, 2007]. However, “environmental perturbations are often vigorous shake-ups, rather than gentle stirrings” [Jansen and Sigmund, 1998]. To account for large, but rare, perturbations, the concept of permanence, or uniform persistence, was introduced in late 1970s [Freedman and Waltman, 1977, Schuster

et al., 1979]. Uniform persistence requires that asymptotically species densities remain uniformly bounded away from extinction. In addition, permanence requires that the system is dissipative i.e. asymptotically species densities remain uniformly bounded from above. Various mathematical approaches exist for verifying permanence [Hutson and Schmitt, 1992, Smith and Thieme, 2011] including topological characterizations with respect to chain recurrence [Butler and Waltman, 1986, Hofbauer and So, 1989], average Lyapunov functions [Hofbauer, 1981, Hutson, 1984, Garay and Hofbauer, 2003], and measure theoretic approaches [Schreiber, 2000, Hofbauer and Schreiber, 2010]. The latter two approaches involve the long-term, per-capita growth rates of species when rare. For discrete-time, unstructured models of the form  $x_{t+1}^i = f_i(x_t)x_t^i$  where  $x_t = (x_t^1, \dots, x_t^n)$  is the vector of population densities at time  $t$ , the long-term growth rate of species  $i$  with initial community state  $x_0 = x$  equals

$$r_i(x) = \limsup_{t \rightarrow \infty} \frac{1}{t} \sum_{s=1}^t \log f_i(x_s).$$

Garay and Hofbauer [2003] showed, under appropriate assumptions, that the system is permanent provided there exist weights  $p_1, \dots, p_n$  associated with each species such that  $\sum_i p_i r_i(x) > 0$  for any initial condition  $x$  with one or more missing species (i.e.  $\prod_i x^i = 0$ ). Intuitively, the community persists if on average the community increases when rare.

The permanence criterion for unstructured populations also extends to structured populations. However, in this case, the long-term growth rate is more complicated. Consider, for example, when both time and the structuring variables are discrete:  $x_{t+1}^i = A_i(x_t)x_t^i$  where  $x_t^i$  is a vector corresponding to the densities of the stages of species  $i$ ,  $x_t = (x_t^1, \dots, x_t^n)$ , and  $A_i$  is a non-negative matrix. Then the long term growth rate  $r_i(x)$  of species  $i$  corresponds to the dominant Lyapunov exponent associated with the matrices  $A_i(x)$  along the population trajectory:

$$r_i(x) = \limsup_{t \rightarrow \infty} \frac{1}{t} \log \|A_i(x_t) \dots A_i(x_1)\|.$$

At the extinction state  $x = 0$ , the long-term growth rate  $r_i(0)$  simply corresponds to the ln of the largest eigenvalue of  $A_i(0)$ . For structured single-species models, Cushing [1998], Kon et al. [2004] proved that  $r_1(0) > 0$  implies permanence. For structured, continuous-time, multiple species models,  $r_i(x)$  can be defined in an analogous manner to the discrete-time case using the fundamental matrix of the variational equation. Hofbauer and Schreiber [2010] showed, under appropriate assumptions, that  $\sum_i p_i r_i(x) > 0$  for all  $x$  in the extinction set is sufficient for permanence. For discrete-time structured models, however, there exists no general proof of this fact. However, Salceanu and Smith [2009a,b, 2010] used long-term growth rates  $r_i(x)$  to establish persistence results for some stage structured, discrete-time models. When both time and the structuring variables are continuous, the models become infinite dimensional and may be formulated as partial differential equations or functional differential equations. Much work has been done in this direction [Hutson and Moran, 1987, Zhao and Hutson, 1994, Thieme, 2009, 2011, Magal et al., 2010, Xu and Zhao, 2003, Jin and Zhao, 2009]. In particular, for reaction diffusion equations, the long-term growth rates correspond to growth rates of semi-groups of linear operators and,  $\sum_i p_i r_i(x) > 0$  for all  $x$  in the extinction set also ensures permanence for these models [Hutson and Moran, 1987, Zhao and Hutson, 1994, Cantrell and Cosner, 2003].

Environmental stochasticity can be a potent force for disrupting population persistence yet maintaining biodiversity. Classical stochastic demography theory for stochastic matrix models  $x_{t+1} = A(t)x_t$  shows that temporally uncorrelated fluctuations in the projection matrices  $A(t)$  reduce the long-term growth rates of populations when rare [Tuljapurkar, 1990, Boyce et al., 2006]. Hence, increases in the magnitude of these uncorrelated fluctuations can shift populations from persisting to asymptotic extinction. Under suitable conditions, the long-term growth rate for these models is given by the limit  $r = \lim_{t \rightarrow \infty} \frac{1}{t} \ln \|A(t) \dots A(1)\|$  with probability one. When  $r > 0$ , the population grows exponentially with probability one for these density-independent models. When  $r < 0$ , the population declines exponentially with probability one. Hardin et al. [1988] and Benaïm and Schreiber [2009], under different sets of assumptions, proved that these conclusions extend to models with compensating density-dependence. However, instead of growing without bound when  $r > 0$ , the populations converge to a positive stationary distribution with probability one. These results, however, do not apply to models with overcompensating density-dependence or, more generally, non-monotonic responses of demography to density.

Environmental stochasticity can promote diversity through the storage effect [Chesson and Warner, 1981, Chesson, 1982] in which asynchronous fluctuations of favorable conditions can allow long-lived species competing for space to coexist. The theory for coexistence in stochastic environments has focused on stochastic difference equations of the form  $x_{t+1}^i = x_t^i f_i(x_t, \xi_{t+1})$  where  $\xi_1, \xi_2, \dots$  are a sequence of independent, identically distributed random variables (for a review see [Schreiber, 2011]). [Schreiber et al., 2011] prove that coexistence, in a suitable sense, occurs provided that  $\sum_i p_i r_i(x) > 0$  with probability for all  $x$  in the extinction set. Similar to the deterministic case, the long-term growth rate of species  $i$  equals  $r_i(x) = \limsup_{t \rightarrow \infty} \frac{1}{t} \sum_{s=1}^t \log f_i(x_s)$ . Here, stochastic coexistence implies that each species spends an arbitrarily small fraction of time near arbitrarily small densities.

Our main result implies that the “community increases when rare” persistence criterion also applies to interacting, structured populations in stochastic environments. Our model, assumptions, and a definition of stochastic persistence are presented in Section 2. Except for a compactness assumption, our assumptions are quite minimal allowing for overcompensating density dependence and correlated environmental fluctuations. Long-term growth rates for these models and our main theorem are stated in Section 3. We apply our results to stochastic models of predator-prey interactions, stage-structured beetle dynamics, and competition in spatial heterogenous environments. The stochastic models for predator-prey interactions are presented in Section 4 and examine to what extent “colored” environmental fluctuations facilitate predator-prey coexistence. In Section 5, we develop precise criteria for persistence and exclusion for structured single species models and apply these results to the classic stochastic model of larvae-pupae-adult dynamics of flour beetles [Costantino et al., 1995, Dennis et al., 1995, Costantino et al., 1997, Henson and Cushing, 1997] and metapopulation dynamics [Harrison and Quinn, 1989, Gyllenberg et al., 1996, Metz and Gyllenberg, 2001, Roy et al., 2005, Hastings and Botsford, 2006, Schreiber, 2010]. We show, contrary to initial expectations, that multiple noise with logarithmic means of zero can facilitate persistence. In Section 6, we examine spatial-explicit lottery models [Chesson, 1985, 2000a,b] to illustrate how spatial and temporal heterogeneity, collectively, mediate coexistence for transitive and intransitive competitive communities.

## 2. MODEL AND ASSUMPTIONS

We study the dynamics of  $m$  interacting populations in a random environment. Each individual in population  $i$  can be in one of  $n_i$  individual states such as their age, size, or location. Let  $X_t^i = (X_t^{i1}, \dots, X_t^{in_i})$  denote the row vector of populations abundances of individuals in different states for population  $i$ .  $X_t^i$  lies in the non-negative cone  $\mathbb{R}_+^{n_i}$ . The *population state* is the row vector  $X_t = (X_t^1, \dots, X_t^m)$  that lies in the non-negative cone  $\mathbb{R}_+^n$  where  $n = \sum_{i=1}^k n_i$ . To account for environment fluctuations, we consider a sequence of random variables,  $\xi_1, \xi_2, \dots, \xi_t, \dots$  where  $\xi_t$  represents the state of the environment at time  $t$ .

To define the population dynamics, we consider projection matrices for each population that depend on the population state and the environmental state. More precisely, for each  $i$ , let  $A_i(X, \xi)$  be a non-negative,  $n_i \times n_i$  matrix whose  $j-k$ -th entry corresponds to the contribution of individuals in state  $j$  to individuals in state  $k$  e.g. individuals transitioning from state  $j$  to state  $k$  or the mean number of offspring in state  $k$  produced by individuals in state  $j$ . Using these projection matrices and the sequence of environmental states, the population dynamic of population  $i$  is given by

$$X_{t+1}^i = X_t^i A_i(\xi_{t+1}, X_t).$$

where  $X_t^i$  multiplies on the left hand side of  $A_i(\xi_{t+1}, X_t)$  as it is a row vector. If we define  $A(\xi, X)$  to be the  $n \times n$  block diagonal matrix  $\text{diag}(A_1(\xi, X), \dots, A_m(\xi, X))$ , then the dynamics of the interacting populations are given by

$$(1) \quad X_{t+1} = X_t A(\xi_{t+1}, X_t).$$

For these dynamics, we make the following assumptions:

- H1:**  $\xi_1, \xi_2, \dots$  is an ergodic stationary sequence in a compact Polish space  $E$ .
- H2:** For each  $i$ ,  $(\xi, X) \mapsto A_i(\xi, X)$  is a continuous map into the space of  $n_i \times n_i$  non-negative matrices.
- H3:** For each population  $i$ , the matrix  $A_i$  has fixed sign structure corresponding to a primitive matrix. More precisely, for each  $i$ , there is a  $n_i \times n_i$  matrix  $P_i$  whose entries are zeros and ones such that all the entries of  $P_i^t$  are positive for some  $t \geq 1$  and for all  $(X, \xi)$  the  $j-k$ -th entry of  $A_i(\xi, X)$  equals zero if and only if  $j$ -th entry  $P_i$  equals zero.
- H4:** There exists a compact set  $S \subset \mathbb{R}_+^n$  such that for all  $X_0 \in \mathbb{R}_+^n$ ,  $X_t \in S$  for all  $t$  sufficiently large.

Our analysis focuses on whether the interacting populations tend, in an appropriate stochastic sense, to be bounded away from extinction. Extinction of one or more population corresponds to the population state lying in the *extinction set*

$$S_0 = \{x \in \mathbb{R}_+^n \mid \prod_i \|x^i\| = 0\}$$

where  $\|x^i\| = \sum_{j=1}^{n_i} x^{ij}$  corresponds to the  $\ell^1$  norm of  $x^i$ . Given  $X_0 = x$ , we define stochastic persistence in terms of the empirical measure

$$(2) \quad \Pi_t^x = \frac{1}{t} \sum_{s=1}^t \delta_{X_s}$$

where  $\delta_y$  denotes a Dirac measure at  $y$ . These empirical measures are random measures describing the distribution of the observed population dynamics up to

time  $t$ . In particular, for any Borel set  $B \subset S$ ,

$$\Pi_t^x(B) = \frac{\#\{1 \leq s \leq t | X_s \in B\}}{t}$$

is the fraction of time that the populations spent time in the set  $B$ . For instance, if we define

$$S_\eta = \{x \in S | \|x^i\| \leq \varepsilon \text{ for some } i\},$$

then  $\Pi_t^x(S_\eta)$  is the fraction of time that the total abundance of some population is less than  $\varepsilon$  given  $X_0 = x$ .

**Definition 2.1.** *For all  $\eta > 0$ , define*

$$S_\eta = \{x \in S : \|x^i\| \leq \eta \text{ for some } i\}.$$

(1) *is stochastically persistent if for all  $\varepsilon > 0$ , there exists  $\eta > 0$  such that*

$$\Pi_t^x(S_\eta) \leq \varepsilon$$

*for  $t$  sufficiently large and all  $x \in S \setminus S_0$ .*

The set  $S_\eta$  corresponds to community states where one or more populations have a density less than  $\eta$ . Therefore, stochastic persistence corresponds to all populations spending an arbitrarily small fraction of time at arbitrarily low densities.

### 3. RESULTS

**3.1. Long-term growth rates and a persistence theorem.** Understanding persistence often involves understanding what happens to each population when it is rare. To this end, we need to understand the propensity of the population to increase or decrease in the long term. Since

$$X_t^i = X_0^i A_i(\xi_1, X_0) A_i(\xi_2, X_1) \dots A_i(\xi_t, X_{t-1}),$$

one might be interested in the long-term “growth” of random product

$$A_i(\xi_1, X_0) A_i(\xi_2, X_1) \dots A_i(\xi_t, X_{t-1})$$

of matrices as  $t \rightarrow \infty$ . One measurement of this long-term growth rate when  $X_0 = x$  is the random variable

$$r_i(x) = \limsup_{t \rightarrow \infty} \frac{1}{t} \log \|A_i(\xi_1, X_0) A_i(\xi_2, X_1) \dots A_i(\xi_t, X_{t-1})\|$$

Population  $i$  is tending to show periods of increase when  $r_i(x) > 0$  and asymptotically decreasing when  $r_i(x) < 0$ . The  $\limsup_{t \rightarrow \infty}$  instead of  $\lim_{t \rightarrow \infty}$  in the definition of  $r_i(x)$  is, in general, necessary. However, as we discuss in Section 3.2, the  $\limsup_{t \rightarrow \infty}$  can be replaced by  $\lim_{t \rightarrow \infty}$  on sets of “full measure”.

An expected, yet useful property of  $r_i(x)$  is that  $r_i(x) \leq 0$  with probability one whenever  $\|x^i\| > 0$ . In words, whenever population  $i$  is present, its per-capita growth rate in the long-term is non-positive. This fact follows from  $X_t^i$  being bounded above for  $t \geq 0$ . Furthermore, on the event of  $\{\limsup_{t \rightarrow \infty} \|X_t^i\| > 0\}$ , we get that  $r_i(x) = 0$  with probability one. In words, if population  $i$ ’s density infinitely often is bounded below some minimal density, then its long-term growth rate is zero as it is not tending to extinction and its densities are bounded from above. Both of these facts are proven in the Appendices.

Our main result extends the persistence conditions discussed in the introduction to stochastic models of interacting, structured populations. Namely, if the community increases on average when rare, then the community persists.

**Theorem 3.1.** *If there exist positive constants  $p_1, \dots, p_m$  such that*

$$(3) \quad \sum_i p_i r_i(x) > 0 \text{ with probability one}$$

*for all  $x \in S_0$ , then (1) is stochastically persistent.*

**3.2. A refinement using invariant measures.** The proof of Theorem 3.1 follows from a more general result that we now present. For this result, we show that one need not verify the persistence condition 3 for all points  $x$  in the extinction set  $S_0$ . It suffices to verify the persistence condition for invariant measures of the process which concentrate on the extinction set.

**Definition 3.2.** *A Borel probability measure  $\mu$  on  $E \times S$  an invariant measure for (1) provided that*

- (i)  $\mathbb{P}[\xi_t \in B] = \mu(B \times S)$  for all Borel sets  $B \subset E$ , and
- (ii) if  $\mathbb{P}[(\xi_0, X_0) \in B] = \mu(B)$  for all Borel sets  $B \subset E \times S$ , then  $\mathbb{P}[(\xi_t, X_t) \in B] = \mu(B)$  for all Borel sets  $B \subset E \times S$  and  $t \geq 0$ .

Condition (i) ensures that invariant measure is consistent with the environmental dynamics. Condition (ii) implies that if the system initially follows the distribution of  $\mu$ , then it follows this distribution for all time. When this occurs, we say  $(\xi_t, X_t)$  is stationary with respect to  $\mu$ . One can think of invariant measures as the stochastic analog of equilibria for deterministic dynamical systems; if the population statistics initially follow  $\mu$ , then it follows  $\mu$  for all time.

When an invariant measure  $\mu$  is statistically indecomposable, it is *ergodic*. More precisely,  $\mu$  is ergodic if  $\mu = \alpha\mu_1 + (1 - \alpha)\mu_2$  for  $0 < \alpha < 1$  and invariant measures  $\mu_i$  implies  $\mu_1 = \mu_2$ .

**Definition 3.3.** *If  $(\xi_t, X_t)$  is stationary with respect to  $\mu$ , the subadditive ergodic theorem implies that  $r_i(X_0)$  is well-defined with probability one. Moreover, we call the expected value*

$$r_i(\mu) = \int \mathbb{E}[r_i(X_0)|X_0 = x, \xi_1 = \xi] \mu(dx, d\xi)$$

*to be long-term growth rate of species  $i$  with respect to  $\mu$ . When  $\mu$  is ergodic, the subadditive ergodic theorem implies that  $r_i(X_0)$  equals  $r_i(\mu)$  for  $\mu$ -almost every  $(X_0, \xi_1)$ .*

With these definitions, we can rephrase Theorem 3.1 in terms of the invasion rates  $r_i(\mu)$  as well as provide an alternative characterization of the coexistence condition.

**Theorem 3.4.** *If one of the following equivalent conditions hold*

- (i)  $r_*(\mu) := \max_{1 \leq i \leq m} r_i(\mu) > 0$  for every invariant probability measure with  $\mu(S_0) = 1$ , or
- (ii) there exist positive constants  $p_1, \dots, p_m$  such that

$$\sum_i p_i r_i(\mu) > 0$$

*for every ergodic probability measure with  $\mu(S_0) = 1$ , or*

- (iii) there exist positive constants  $p_1, \dots, p_m$  such that

$$\sum_i p_i r_i(x) > 0 \text{ with probability one}$$

*for all  $x \in S_0$*

then (1) is stochastically persistent.

To illustrate the applicability of Theorem 3.4, we apply the coexistence criterion to stochastic models of predator-prey interactions, stage-structured populations with over-compensating density-dependence, and transitive and intransitive competition in spatially heterogeneous environments.

#### 4. PREDATOR-PREY DYNAMICS IN AUTO-CORRELATED ENVIRONMENTS

For unstructured populations, Theorem 3.4 extends Schreiber et al. [2011]’s criteria for persistence to temporally correlated environments. These temporal correlations can have substantial consequences for coexistence as we illustrate now for a stochastic model of predator-prey interactions. In the absence of the predator, the prey, with density  $N_t$  at time  $t$ , exhibits a noisy Beverton-Holt dynamic given by

$$(4) \quad N_{t+1} = \frac{R_{t+1}N_t}{1 + aN_t}$$

where  $R_t$  is a stationary, ergodic sequence of random variables corresponding to the intrinsic fitness of the prey at time  $t$ , and  $a > 0$  corresponds to the strength of intraspecific competition. To ensure the persistence of the prey in the absence of the predator, we assume that  $\mathbb{E}[\ln R_1] > 0$  and  $\mathbb{E}[\ln R_1] < \infty$ . Under these assumptions, Theorem 1 of Benaïm and Schreiber [2009] implies that  $N_t$  converges in distribution to a positive random variable  $\widehat{N}$  whenever  $N_0 > 0$ . Moreover, the empirical measures  $\Pi_t^{(N,P)}$  with  $N > 0, P = 0$  converge almost surely to the law  $\nu$  of the random vector  $(\widehat{N}, 0)$  i.e. the invariant probability measure satisfying  $\nu(A) = \mathbb{P}[(\widehat{N}, 0) \in A]$  for any Borel set  $A \subset \mathbb{R}_+^2$ .

Let  $P_t$  be the density of predators at time  $t$  and  $\exp(-bP_t)$  be the fraction of prey that “escape” predation during generation  $t$  where  $b$  is the predator attack rate. The mean number of predators offspring produced per consumed prey is  $c$ , while  $s$  corresponds to the fraction of predators that survive to the next time step. Following May and Hassell, we get the following model of predator-prey dynamics

$$(5) \quad \begin{aligned} N_{t+1} &= \frac{R_{t+1}N_t}{1 + aN_t} \exp(-bP_t) \\ P_{t+1} &= cN_t(1 - \exp(-bP_t)) + sP_t \end{aligned}$$

To ensures that (5) satisfies the assumptions of Theorem 3.1, we assume  $R_t$  takes values in the half open interval  $(0, R^*]$ . Since  $N_{t+1} \leq R_{t+1}/a \leq R^*/a$  and  $P_{t+1} \leq cN_t + sP_t \leq R^*/a + sP_t$ ,  $X_t = (N_t, P_t)$  eventually enters and remains in the compact set

$$S = [0, R^*/a] \times [0, \theta R^*/(a(1-s))].$$

To apply Theorem 3.1, we need to evaluate  $r_i((N, P))$  for all  $N \geq 0, P \geq 0$  with either  $N = 0$  or  $P = 0$ . Since  $(0, P_t)$  converges to  $(0, 0)$  with probability one whenever  $P_0 \geq 0$ , we have  $r_1((0, P)) = \mathbb{E}[\ln R_t] > 0$  and  $r_2((0, P)) = \ln s < 0$  whenever  $P \geq 0$ . Since  $\Pi_t^{(N,0)}$  with  $N > 0$  converges almost surely to  $\nu$ , we get  $r_1((N, 0)) = 0$  by Proposition 8.18 and

$$(6) \quad r_2((N, 0)) = \mathbb{E} \left[ \ln \left( cb\widehat{N} + s \right) \right] = \int \ln(cbx + s) \nu(dx)$$

By choosing  $p_1 = 1 - \varepsilon$  and  $p_2 = \varepsilon > 0$  for  $\varepsilon$  sufficiently small (e.g.  $0.5\mathbb{E}[\ln R_t]/(\mathbb{E}[\ln R_t] - \ln s)$ ), we have  $\sum_i p_i r_i((N, P)) > 0$  whenever  $NP = 0$  and

$$(7) \quad \mathbb{E} \left[ \ln \left( cb\hat{N} + s \right) \right] > 0.$$

Namely, the predator and prey coexist whenever the predator can invade the prey-only system.

To see how temporal correlations influence whether the persistence criterion (7) holds or not, consider an environment that fluctuates randomly between good and bad years for the prey. On good years,  $R_t$  takes on the value  $r_{good}$ , while in bad years it takes on the value  $R_{bad}$ . Let the transitions between good and bad years be determined by a Markov chain where the probability of going from a bad year to a good year is  $p$  and the probability of going from a good year to a bad year is  $q$ . For simplicity, we assume that  $p = q$  in which case half of the years are good and half of the years are bad in the long run. Under these assumptions, the persistence criterion  $\mathbb{E}[\ln R_1] > 0$  for the prey is  $\ln(R_{good}R_{bad}) > 0$ .

To estimate the left-hand side of (7), we consider the limiting cases of strongly negatively correlated environments ( $p \approx 1$ ) and strongly positively correlated environments ( $p \approx 0$ ). When  $p \approx 1$ , the environmental dynamics are nearly periodic switching nearly every other time step between good and bad years. Hence, one can approximate  $\hat{N}$  by considering the positive, globally stable fixed point of

$$\begin{aligned} x_{t+2} &= \frac{R_{good}x_{t+1}}{1 + ax_{t+1}} \\ &= \frac{R_{good}R_{bad}x_t/(1 + ax_t)}{1 + a(R_{bad}x_t/(1 + ax_t))} \\ &= \frac{R_{good}R_{bad}x_t}{1 + a(1 + R_{bad})x_t} \end{aligned}$$

which is given by  $\frac{R_{good}R_{bad}-1}{a(1+R_{bad})}$ . Hence, if  $p \approx 1$ , then  $\hat{N}$  approximately puts half of its weight on  $\frac{R_{good}R_{bad}-1}{a(1+R_{bad})}$  and half of its weight on  $\frac{R_{good}R_{bad}-1}{a(1+R_{good})}$  and the persistence criterion (7) is approximately

$$(8) \quad \frac{1}{2} \ln \left( bc \frac{R_{good}R_{bad} - 1}{a(1 + R_{bad})} + s \right) + \frac{1}{2} \ln \left( bc \frac{R_{good}R_{bad} - 1}{a(1 + R_{good})} + s \right) > 0.$$

Next, consider the case that  $p \approx 0$  in which there are long runs of good years and long runs of bad years. Due to these long runs, one expects that half time  $\hat{N}$  is near the value  $(R_{good} - 1)/a$  and half the time it is near the value  $\max\{(R_{bad} - 1)/a, 0\}$ . If  $R_{bad} > 1$ , then the persistence criterion is approximately

$$(9) \quad \frac{1}{2} \ln \left( bc \frac{R_{good} - 1}{a} + s \right) + \frac{1}{2} \ln \left( bc \frac{R_{bad} - 1}{a} + s \right) > 0$$

Relatively straightforward algebraic manipulations (e.g. exponentiating the left hand sides of (8) and (9) and multiplying by  $(1 + R_{bad})(1 + R_{good})$ ) show that the left hand side of (8) is always greater than the left hand side of (9).

**Biological Interpretation 4.1.** *Positive autocorrelations, by increasing variability in prey density, hinders predator establishment and, thereby, coexistence of the predator and prey. In contrast, negative auto-correlations by reducing variability in prey density can facilitate predator-prey coexistence (Fig. 1).*

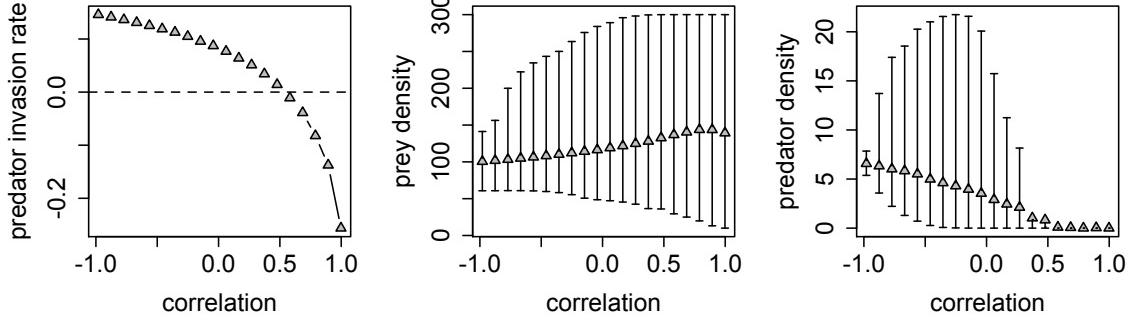


FIGURE 1. Effect of temporal autocorrelations on predator-prey coexistence in a Markovian environment. In (a), the long-term growth rate  $r_2((N, 0))$  with  $N > 0$  of the predator when rare is plotted as a function of the temporal autocorrelation between good and bad reproductive years for the prey. In (b) and (c), the mean and interquartile ranges of long-term distribution of prey and predator densities are plotted as function of the temporal autocorrelation. Parameters:  $R_{good} = 4$ ,  $R_{bad} = 1.1$ ,  $a = 0.01$ ,  $c = 1$ ,  $s = 0.1$ ,  $b = 0.01$ .

## 5. APPLICATION TO STRUCTURED SINGLE SPECIES MODELS

For single species models with negative-density dependence, we can prove sufficient and necessary conditions for stochastic persistence. The following theorem implies that stochastic persistence occurs if the long-term growth rate  $r_1(0)$  when rare is positive and asymptotic extinction occurs with probability one if this long-term growth rate is negative.

**Theorem 5.1.** *Assume that  $m = 1$  (i.e. there is one species), **H1-H4** hold and the entries of  $A(\xi, x) = A_1(\xi, x)$  are non-increasing functions of  $x$ . If  $r_1(0) > 0$ , then*

$$(10) \quad X_{t+1} = X_t A(\xi_{t+1}, X_t)$$

*is stochastically persistent. If  $r_1(0) < 0$ , then  $\lim_{t \rightarrow \infty} X_t = (0, 0, \dots, 0)$  with probability one.*

*Proof.* The first statement of this theorem follows from Theorem 3.1.

Assume that  $r_1(0) < 0$ . Provided that  $X_0$  is nonnegative with at least one strictly positive entry, Ruelle's stochastic version of the Perron Frobenius Theorem [Ruelle, 1979a, Proposition 3.2] and the entries of  $A(\xi, x)$  being non-increasing in  $x$  imply

$$\lim_{t \rightarrow \infty} \frac{1}{t} \log \|X_t\| \leq \lim_{t \rightarrow \infty} \frac{1}{t} \log \|X_0 A(\xi_t, 0) \dots A(\xi_1, 0)\| = r(0) < 0$$

with probability one. Hence,  $\lim_{t \rightarrow \infty} X_t = (0, \dots, 0)$  with probability one.  $\square$

Theorem 5.1 extends Theorem 1 of Benaïm and Schreiber [2009] as it allows for over-compensating density dependence and makes no assumptions about differentiability of  $x \mapsto A(\xi, x)$ . To illustrate its utility, we apply this result to the larvae-pupae-adult model of flour beetles and a metapopulation model.

**5.1. A stochastic Larvae-Pupae-Adult model for flour beetles.** An important, empirically validated model in ecology is the “Larvae-Pupae-Adult” (LPA) model which describes flour beetle population dynamics [Costantino et al., 1995, Dennis et al., 1995, Costantino et al., 1997]. The model keeps track of the densities  $\ell_t, p_t, a_t$  of larvae, pupae, and adults at time  $t$ . Adults produce  $b$  eggs each time step. These eggs are cannibalized by adults and larvae at rates  $c_{ea}$  and  $c_{el}$ , respectively. The eggs escaping cannibalism become larvae. A fraction  $\mu_l$  of larvae die at each time step. Larvae escaping mortality become pupae. Pupae are cannibalized by adults at a rate  $c_{pa}$ . Those individuals escaping cannibalism become adults. A fraction  $\mu_a$  of adults survive through a time step. These assumptions result in a system of three difference equations

$$(11) \quad \begin{aligned} \ell_{t+1} &= b a_t \exp(-c_{el}\ell_t - c_{ea}a_t) \\ p_{t+1} &= (1 - \mu_l)\ell_t \\ a_{t+1} &= (p_t \exp(-c_{pa}a_t) + (1 - \mu_a)a_t) \end{aligned}$$

Environmental fluctuations has been included in these models in at least two ways. Dennis et al. [1995] assumed that each stage experienced random fluctuations due to multiplicative factors  $\exp(\xi_t^l), \exp(\xi_t^p), \exp(\xi_t^a)$  such that  $\xi_t^i$  for  $i = l, p, a$  are normally distributed with mean zero i.e. on the log-scale the average effect of environmental fluctuations are accounted for by the deterministic model. Alternatively, Henson and Cushing [1997] considered periodic fluctuations in cannibalism rates due to fluctuations in the size  $V_t$  of the habitat i.e. the volume of the flour. In particular, they assumed that  $c_i = \kappa_i/V_t$  for  $i = l, a, p$ , for positive constants  $\kappa_i$ . If we include both of these stochastic effects into the deterministic model, we arrive at the following system of random difference equations.

$$(12) \quad \begin{aligned} \ell_{t+1} &= b a_t \exp(-\kappa_{el}\ell_t/V_{t+1} - \kappa_{ea}a_t/V_{t+1} + \xi_t^l) \\ p_{t+1} &= (1 - \mu_l)\ell_t \exp(\xi_t^p) \\ a_{t+1} &= (p_t \exp(-\kappa_{pa}a_t/V_{t+1}) + (1 - \mu_a)a_t) \exp(\xi_t^a) \end{aligned}$$

Regarding these equations, we can use Theorem 3.4 to prove the following persistence result. When  $\xi_t^i = 0$  with probability one for  $i = l, p, a$ , this theorem can be viewed as a stochastic extension of Theorem 4 of Henson and Cushing [1997] for periodic environments.

**Theorem 5.2.** *Assume  $c^i > 0$  for  $i = l, p, a$ ,  $\mu_i \in (0, 1)$  for  $i = l, a$ ,  $\xi_t^l, \xi_t^p, \xi_t^a$ , and  $V_t$  are ergodic and stationary sequences such that  $\xi_t^i, \log V_t \in (-M, M)$  for  $i = l, p, a$  and some  $M > 0$ , and  $(1 - \mu_a) \exp(\xi_t^a) \in [0, 1 - \delta]$  for some  $\delta > 0$  with probability one. Then there exists a critical birth rate  $b_{crit} > 0$  such that*

**Extinction:** *If  $b < b_{crit}$ , then  $X_t = (\ell_t, p_t, a_t)$  converges almost surely to  $(0, 0, 0)$  as  $t \rightarrow \infty$ .*

**Stochastic persistence:** *If  $b > b_{crit}$ , then the LPA model is stochastically persistent.*

Moreover, if  $\xi_t^l = \xi_t^a = \xi_t^p$  with probability one and  $\mathbb{E}[\xi_t^l] = 0$ , then  $b_{crit} = \mu_a/(1 - \mu_l)$ .

**Remark.** The assumption that  $\xi_t^i$  are compactly supported formerly excludes the normal distributions used by Dennis et al. [1995]. However, truncated normals with a very large  $M$  can approximate the normal distribution arbitrarily well. The assumption  $(1 - \mu_a) \exp(\xi_t^a) \in [0, 1 - \delta]$  for some  $\delta > 0$  is more restrictive. However, from a biological standpoint, it is necessary as this term corresponds to the fraction

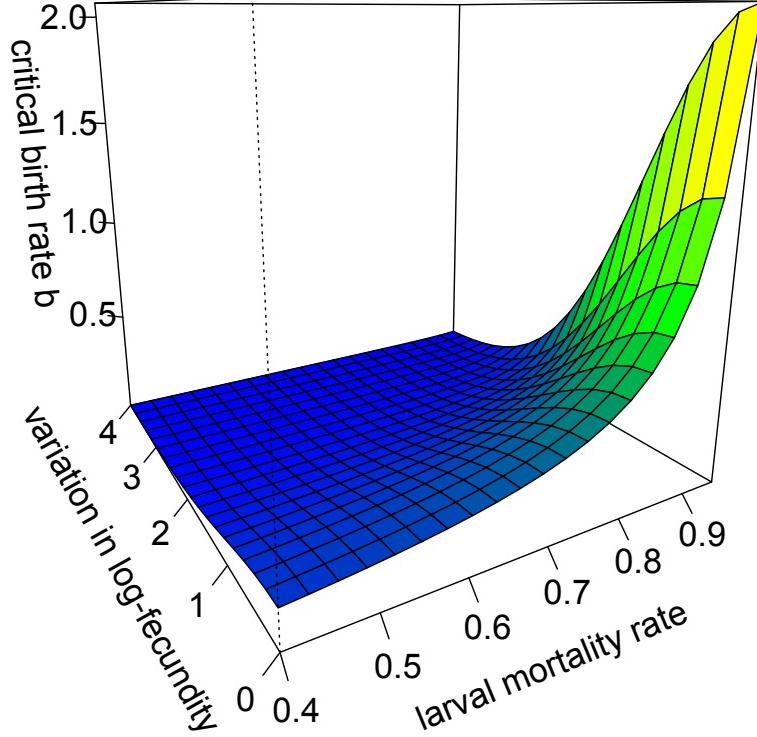


FIGURE 2. Effects fluctuations in fecundity and larval survival on the critical birth rate  $b$  required for persistence.  $\xi_t^l$  is normally distributed with mean 0 and shown variance,  $\xi_t^a = \xi_t^p = 0$  for all  $t$  and  $\mu_a = 0.1034$  (the value found in Table 1D in Costantino et al. [1995]).

of adults surviving to the next time step. None the less, we conjecture that the conclusions of Theorem 5.2 hold when  $\xi_t^i$  are normally distributed with mean 0.

Theorem 5.2 implies that including multiplicative noise with log-mean zero has no effect on the deterministic persistence criterion when  $\xi_t^l = \xi_t^p = \xi_t^a$  with probability one. However, when these random variables are not perfectly correlated, we conjecture that this form of multiplicative noise always decreases the critical birth rate (Fig. 2). To provide some mathematical evidence for this conjecture, we compute a small noise approximation for the invasion rate  $r_1(\delta_0)$  when population is rare [Ruelle, 1979a; Tuljapurkar, 1990]. Let

$$B_t = \begin{pmatrix} 0 & (1 - \mu_l) \exp(\xi_t^p) & 0 \\ 0 & 0 & \xi_t^a \\ b\xi_t^l & 0 & (1 - \mu_a) \exp(\xi_t^a) \end{pmatrix}$$

be the linearization of the stochastic LPA model (12) at  $(L, P, A) = (0, 0, 0)$ . Assume that  $\xi_t^i = \bar{\xi}^i + \varepsilon Z_t^i$  where  $\mathbb{E}[Z_t^i] = 0$  and  $\mathbb{E}[(Z_t^i)^2] = 1$ . A second order approximation

to  $B_t$  in  $\varepsilon$  is

$$B_t \approx \underbrace{\begin{pmatrix} 0 & (1 - \mu_l) & 0 \\ 0 & 0 & 1 \\ b & 0 & (1 - \mu_a) \end{pmatrix}}_{=B} \left( I + \varepsilon \text{diag}\{\xi_t^l, \xi_t^p, \xi_t^a\} + \varepsilon^2 \text{diag}\{\xi_t^l, \xi_t^p, \xi_t^a\}^2 / 2 \right).$$

Let  $v$  and  $w$  be the left and right Perron-eigenvectors of  $B$  such that  $\sum_i v_i = 1$  and  $\sum_i v_i w_i = 1$ . Let  $r_0$  be the associated Perron eigenvalue of  $B$ . Provided the  $Z_t^i$  are independent in time, a small noise approximation for the stochastic growth rate of the random products of  $B_t$  is

$$(13) \quad r_*(\delta_0) \approx \log r_0 + \frac{\varepsilon^2}{2r_0^2} \left( \mathbb{E} \left[ \sum_i v_i w_i (Z_t^i)^2 \right] - \mathbb{E} \left[ \left( \sum_i v_i w_i Z_t^i \right)^2 \right] \right)$$

By Cauchy-Schwartz,

$$\begin{aligned} \mathbb{E} \left[ \left( \sum_i v_i w_i Z_t^i \right)^2 \right] &\leq \mathbb{E} \left[ \sum_i v_i^2 w_i^2 (Z_t^i)^2 \right] \\ &\leq \mathbb{E} \left[ \sum_i v_i w_i (Z_t^i)^2 \right] \end{aligned}$$

where the second line follows from  $0 \leq v_i w_i \leq 1$  for all  $i$ . It follows that the order  $\varepsilon^2$  correction term in (13) is non-negative and equals zero if and only if  $Z_t^l = Z_t^p = Z_t^a$  with probability one. Therefore, “small” multiplicative noise (with log-mean zero) which isn’t perfectly correlated across the stages increases the stochastic growth rate and, therefore, decreases the critical birth rate  $b_{crit}$  required for stochastic persistence.

**Biological Interpretation 5.3.** *For the LPA model, there is a critical mean fecundity, above which the population persists and below which the population goes asymptotically to extinction. Positive correlations between the survival rates of the different stages increases this critical mean fecundity. Negative correlations between the survival rates lower the critical mean fecundity.*

*Proof of Theorem 5.2.* We begin by verifying **H1–H4**. **H1** and **H2** follows from our assumptions. To verify **H3**, notice that the sign structure of nonlinear projection matrix  $A_t(\xi, X)$  for (12) is given by

$$C = \begin{pmatrix} 0 & 1 & 0 \\ 0 & 0 & 1 \\ 1 & 0 & 1 \end{pmatrix}$$

Since

$$C^4 = \begin{pmatrix} 1 & 1 & 1 \\ 1 & 1 & 2 \\ 2 & 1 & 3 \end{pmatrix}$$

$A_t(\xi, X)$  has the sign structure of the primitive matrix  $C$  for all  $\xi, X$  and  $t$ . Finally, to verify **H4**, define

$$K = b e^{2M-1} / \kappa_{ea}$$

Then

$$\ell_{t+1} \leq b a_t \exp(-\kappa_{ea} a_t / V_{t+1} + \xi_t^l) \leq b a_t \exp(-\kappa_{ea} a_t \exp(-M) + M) \leq K$$

for all  $t \geq 0$ . Therefore,  $\ell_t \leq K$  for  $t \geq 1$ . Hence,

$$p_t \leq \ell_{t-1} e^M \leq K e^M$$

for all  $t \geq 2$ . Hence,

$$a_{t+1} \leq p_t e^M + (1 - \delta) a_t$$

for all  $t \geq 2$ . Hence  $a_t \leq K e^{3M}/\delta$  for  $t$  sufficiently large. The compact forward invariant set  $S = [0, K] \times [0, K e^M] \times [0, K e^{3M}]/\delta$  satisfies **H3**.

At low density we get

$$B_t = A(\xi_t, 0) = \begin{pmatrix} 0 & (1 - \mu_l) \exp(\xi_t^p) & 0 \\ 0 & 0 & \xi_t^a \\ b \xi_t^l & 0 & (1 - \mu_a) \exp(\xi_t^a) \end{pmatrix}$$

Define  $r(b)$  to be the dominant Lyapunov exponent of the random products of  $B_1, B_2, \dots$ . Theorem 3.1 of Ruelle [1979a] implies that  $r(b)$  is differentiable for  $b > 0$  and the derivative is given by (see, e.g., section 4.1 of Ruelle [1979a]) equals

$$r'(b) = \mathbb{E} \left[ \frac{v_t(b) E_{31} w_{t+1}(b)}{v_t(b) B_t(b) w_{t+1}(b)} \right] > 0$$

where  $v_t(b), w_t(b)$  are the normalized left and right invariant sub-bundles associated with  $B_t(b)$  and  $E_{31}$  is the matrix with 1 in the  $3 - 1$  entry and 0 entries otherwise. Since the numerators and denominators in the expectation are always positive,  $r(b)$  is a strictly increasing function of  $b$ . Since  $\lim_{b \rightarrow 0} r(b) = -\infty$  and  $\lim_{b \rightarrow \infty} r(b) = \infty$ , there exists  $b_{crit} > 0$  such that  $r(b) < 0$  for  $b < b_{crit}$  and  $r(b) > 0$  for  $b > b_{crit}$

If  $b > b_{crit}$ , then  $r(b) > 0$  and Theorem 5.1 implies that (12) is stochastically persistent. On the other hand, if  $b < b_{crit}$ , then  $r(b) < 0$  and Theorem 5.1 implies that  $(\ell_t, p_t, a_t)$  converges to  $(0, 0, 0)$  with probability one as  $t \rightarrow \infty$ .

The final assertion about the stochastic LPA model follows from observing that if  $\xi_t^a = \xi_t^l = \xi_t^a$  with probability one for all  $t$ , then

$$B_t = \begin{pmatrix} 0 & (1 - \mu_l) & 0 \\ 0 & 0 & 1 \\ b & 0 & (1 - \mu_a) \end{pmatrix} \exp(\xi_t^l)$$

with probability one. Hence,  $r(b) = \log r_0(b) + \mathbb{E}[\xi_t^l]$  where  $r_0(b)$  is the dominant eigenvalue of the deterministic matrix

$$\begin{pmatrix} 0 & (1 - \mu_l) & 0 \\ 0 & 0 & 1 \\ b & 0 & (1 - \mu_a) \end{pmatrix}$$

Therefore, if  $\mathbb{E}[\log \xi_t^l] = 0$ , then  $r(b) = \log r_0(b)$ . Using Jury conditions Henson and Cushing [1997] showed that  $r_0(b) > 1$  if  $b > \mu_a/(1 - \mu_l)$  and  $r_0(b) < 1$  if  $b < \mu_a/(1 - \mu_l)$ . Hence, when  $\xi_t^l = \xi_t^p = \xi_t^a$  with probability one and  $\mathbb{E}[\xi_t^l] = 0$ ,  $b_{crit}$  equals  $\mu_a/(1 - \mu_l)$  as claimed.  $\square$

**5.2. Metapopulation dynamics.** Interactions between movement and spatio-temporal heterogeneities determine how quickly a population grows or declines. Understanding the precise nature of these interactive effects is a central issue in population biology receiving increasing attention from theoretical, empirical, and applied perspectives [Petchey et al., 1997, Lundberg et al., 2000, Gonzalez and Holt, 2002, Schmidt, 2004, Roy et al., 2005, Boyce et al., 2006, Hastings and Botsford, 2006, Matthews and Gonzalez, 2007, Schreiber, 2010].

A basic model accounting for these interactions involves a population living in a patchy environment with  $n$  patches. Let  $X_t^i$  be the number of individuals in patch  $i$  at time  $t$ . Assuming Ricker density-dependent feedbacks at the patch scale, the fitness of an individual in patch  $i$  is  $\lambda_t^i \exp(-\alpha_i X_t^i)$  at time  $t$ , where  $\lambda_t^i$  is the maximal fitness and  $\alpha_i > 0$  measures the strength of intraspecific competition. Let  $d_{ij}$  be the fraction of the population from patch  $i$  that disperse to patch  $j$ . Under these assumptions, the population dynamics are given by

$$(14) \quad X_{t+1}^i = \sum_{j=1}^n d_{ji} \lambda_t^j X_t^j \exp(-\alpha_j X_t^j) \quad i = 1, \dots, n.$$

To write this model more compactly, let  $F(X_t, \lambda_t)$  be the diagonal matrix with diagonal entries  $\lambda_1 \exp(-\alpha_1 X_t^1), \dots, \lambda_n \exp(-\alpha_n X_t^n)$ , and  $D$  be the matrix whose  $i$ - $j$ th entry is given by  $d_{ij}$ . With this notation, (14) simplifies to

$$X_{t+1} = X_t F(X_t, \lambda_t) D$$

Provided the  $\lambda_t^i$  are ergodic and stationary,  $\lambda_t^i$  take values in a positive compact interval  $[\lambda_*, \lambda^*]$  and  $D$  is a primitive matrix, then the hypotheses of Theorem 5.1 hold. In particular, stochastic persistence occurs only if  $r_1(0)$ , corresponding to the dominant Lyapunov exponent of the random matrix product  $F(0, \lambda_t)D \dots F(0, \lambda_1)D$ , is positive.

When populations are fully mixing (i.e.  $d_{ij} = v_j$  for all  $i, j$ ), Metz et al. [1983] derived a simple expression for  $r_1(0)$  given by

$$(15) \quad r_1(0) = \mathbb{E} \left[ \log \left( \sum_{i=1}^n v_i \lambda_t^i \right) \right]$$

i.e. the temporal log-mean of the spatial arithmetic mean. Owing to the concavity of the log function, Jensen's inequality applied to the spatial and temporal averages in (15) yields

$$\log \left( \sum_{i=1}^n v_i \mathbb{E}[\lambda_t^i] \right) > \mathbb{E} \left[ \log \left( \sum_{i=1}^n v_i \lambda_t^i \right) \right] > \sum_{i=1}^n v_i \mathbb{E}[\log \lambda_t^i]$$

The second inequality implies that dispersal can mediate persistence as  $r_1(0)$  can be positive despite all local growth rates  $\mathbb{E}[\log \lambda_t^i]$  being negative. However, the first inequality implies that dispersal-mediated persistence for well-mixed populations requires that the expected fitness  $\mathbb{E}[\lambda_t^i]$  is greater than one in at least one patch. Schreiber [2010] developed first-order corrections to (15) for partially mixing populations where  $d_{ij} = v_j \pm \varepsilon$ . A brief discussion of the implications of these results are provided in the Discussion.

**Biological Interpretation 5.4.** *Metapopulations with density-dependent growth can stochastically persist despite all local populations being extinction prone in the absence of immigration.*

## 6. APPLICATIONS TO COMPETING SPECIES IN SPACE

The roles of spatial and temporal heterogeneity in maintaining diversity is a fundamental problem of practical and theoretical interest in population biology [Chesson, 2000a,b, Loreau et al., 2003, Mouquet and Loreau, 2003, Davies et al., 2005]. To examine the role of both forms of heterogeneity in maintaining diversity of competitive communities, we consider lottery-type models of  $m$  competing populations in

a landscape consisting of  $n$  patches. For these models, competition for vacant space determines the within patch dynamics, while dispersal between the patches couples the local dynamics. After describing a general formulation of these models for an arbitrary number of species with potentially frequency-dependent interactions, we illustrate how to apply our results to case of two competing species and three competing species exhibiting an intransitive, rock-paper-scissor like dynamic.

**6.1. Formulation of the general model.** To describe the general model, let  $X_t^{ir}$  denote the fraction of patch  $r$  occupied by population  $i$  at time  $t$ . At each time step, a fraction  $\varepsilon > 0$  of individuals die in each patch. The sites emptied by the dying individuals get randomly assigned to progeny in the patch. Birth rates within each patch are determined by local pair-wise interactions. Let  $\xi_t^{ij}(r)$  be the “payoff” to strategy  $i$  interacting with strategy  $j$  in patch  $r$  at time  $t$ . Let

$$\Xi_t(r) = \left( \xi_t^{ij}(r) \right)_{1 \leq i,j \leq m}$$

be the payoff matrix for patch  $r$ . The total number of progeny produced by an individual playing strategy  $i$  in patch  $r$  is  $\sum_j \xi_t^{ij} X_t^{jr}$ . Progeny disperse between patches with  $d_{rs}$  the fraction of progeny dispersing from patch  $s$  to patch  $r$ . Under these assumptions, the spatial-temporal dynamics of the competing populations are given by

$$(16) \quad X_{t+1}^{ir} = \varepsilon \frac{\sum_s d_{rs} \sum_j \xi_t^{ij}(s) X_t^{is} X_t^{js}}{\sum_s d_{rs} \sum_{j,l} \xi_t^{ij}(s) X_t^{ls} X_t^{js}} + (1 - \varepsilon) X_t^{ir}.$$

Let  $A_i(\xi, X)$  be the matrix whose  $r - s$  entry is given by

$$\varepsilon \frac{d_{rs} \sum_j \xi_t^{ij}(s) X_t^{js}}{\sum_s' d_{rs'} \sum_{j,l} \xi_t^{ij}(s') X_t^{ls'} X_t^{js'}}$$

for  $r \neq s$ , and

$$\varepsilon \frac{d_{rs} \sum_j a^{ij}(s) X_t^{js}}{\sum_s' d_{rs'} \sum_{j,l} a^{ij}(s') X_t^{ls'} X_t^{js'}} + 1 - \varepsilon$$

for  $r = s$ . With these definitions, (16) is of the form of our models (1).

To illustrate the insights that can be gained from a persistence analysis of these models, we consider two special cases. The first case is a spatially explicit version of Chesson and Warner [1981]’s lottery model. The second case is a spatial version of a stochastic rock-paper-scissor game. For both of these examples, we assume that a fraction  $d$  of all progeny disperse randomly to all patches and the remaining fraction  $1 - d$  do not disperse. Under this assumption, we get  $d_{sr} = d/(m - 1)$  for  $s \neq r$  and  $d_{ss} = 1 - d$ . These populations are fully mixing when  $d = \frac{m-1}{m}$  in which case  $d_{sr} = \frac{1}{m}$  for all  $s, r$ .

**6.2. A spatially-explicit lottery model.** The lottery model of Chesson and Warner [1981] assumes that the competing populations do not exhibit frequency dependent interactions. More specifically, the “payoffs”  $\xi_t^{ij}(r) = \xi_t^i(r)$  for all  $i, j$  are independent of the frequencies of the other species. Consequently, the model takes on a simpler form

$$(17) \quad X_{t+1}^{ir} = \varepsilon \frac{\sum_s d_{rs} \xi_t^i(s) X_t^{is}}{\sum_s d_{rs} \sum_j \xi_t^j(s) X_t^{js}} + (1 - \varepsilon) X_t^{ir}.$$

where  $d_{rs} = \frac{d}{m-1}$  for  $r \neq s$  and  $d_{ss} = 1 - d$ .

For two competing species (i.e.  $m = 2$ ), define  $z_1 = (1, \dots, 1, 0, \dots, 0)$  and  $z_2 = (0, \dots, 0, 1, \dots, 1)$  in which case the extinction set is  $S_0 = \{z_1, z_2\}$ . Theorem 3.1 implies that a sufficient condition for stochastic persistence is the existence of positive weights  $p_1, p_2$  such that

$$p_1 r_1(z_1) + p_2 r_2(z_1) > 0 \text{ and } p_1 r_1(z_2) + p_2 r_2(z_2) > 0$$

Proposition 8.18 implies that  $r_1(z_1) = r_2(z_2) = 0$ . Hence, the persistence criterion simplifies to

$$r_1(z_2) > 0 \text{ and } r_2(z_1) > 0.$$

In other words, persistence occurs if each species has a positive invasion rate when rare.

To get some biological intuition from the mutual invisibility criterion, we consider the limiting cases of relatively sedentary populations (i.e.  $d \approx 0$ ) and highly dispersive populations (i.e.  $d \approx 1$ ). In these cases, we get explicit expressions for the realized per-capita growth rates  $r_i(z_j)$  that simplify further for short-lived (i.e.  $\varepsilon \approx 1$ ) and long-lived (i.e.  $\varepsilon \approx 0$ ) species. Our analytical results are illustrated numerically in Fig. 3.

**6.2.1. Relatively sedentary populations.** When populations are completely sedentary (i.e.  $d = 0$ ), the projection matrix  $A^2(\xi, (1, \dots, 1, 0, \dots, 0))$  reduces to diagonal matrices whose  $r$ -th diagonal entry equals

$$\varepsilon \frac{\xi_t^2(r)}{\xi_t^1(r)} + 1 - \varepsilon$$

The dominant Lyapunov exponent in this limiting case is given by

$$r_2(z_1) = \max_r \mathbb{E} \left[ \log \left( \varepsilon \frac{\xi_t^2(r)}{\xi_t^1(r)} + 1 - \varepsilon \right) \right].$$

Proposition 3 from Benaïm and Schreiber [2009] implies that  $r_2(z_1)$  is a continuous function of  $d$ . Consequently,  $r_2(z_1)$  is positive for small  $d > 0$  provided that  $\mathbb{E} \left[ \log \left( \varepsilon \frac{\xi_t^2(r)}{\xi_t^1(r)} + 1 - \varepsilon \right) \right]$  is strictly positive for some patch  $r$ . Similarly,  $r_1(z_2)$  is positive for small  $d > 0$  provided that  $\mathbb{E} \left[ \log \left( \varepsilon \frac{\xi_t^1(r)}{\xi_t^2(r)} + 1 - \varepsilon \right) \right]$  is strictly positive for some patch  $r$ . Thus, coexistence for small  $d > 0$  occurs if

$$\max_r \mathbb{E} \left[ \log \left( \varepsilon \frac{\xi_t^2(r)}{\xi_t^1(r)} + 1 - \varepsilon \right) \right] > 0 \text{ and } \max_r \mathbb{E} \left[ \log \left( \varepsilon \frac{\xi_t^1(r)}{\xi_t^2(r)} + 1 - \varepsilon \right) \right] > 0.$$

When  $\varepsilon \approx 1$  or  $\varepsilon \approx 0$ , we get more explicit forms of this coexistence condition. When the populations are short-lived ( $\varepsilon \approx 1$ ), the coexistence condition simplifies to  $\mathbb{E}[\log a_t^1(r)] > \mathbb{E}[\log a_t^2(r)]$  and  $\mathbb{E}[\log a_t^2(s)] > \mathbb{E}[\log a_t^1(s)]$  for some patches  $r \neq s$ . If the log-fecundities  $\log a_t^i(r)$  are normally distributed with mean  $\mu_i(r)$  and variance  $\sigma_i^2(r)$ , this coexistence conditions becomes

$$\mu_1(r) > \mu_2(r) \text{ and } \mu_2(s) > \mu_1(s)$$

for some patches  $r \neq s$ . In particular, coexistence requires that each species has at least one patch in which they have a higher geometric mean in their reproductive output.

When the populations are long lived ( $\varepsilon \approx 0$ ) and relatively sedentary ( $d \approx 0$ ), the coexistence condition simplifies to

$$\mathbb{E} \left[ \frac{\xi_t^2(r)}{\xi_t^1(r)} \right] > 1 \text{ and } \mathbb{E} \left[ \frac{\xi_t^1(s)}{\xi_t^2(s)} \right] > 1$$

for some patches  $r, s$ . Unlike short-lived populations, it is possible that both inequalities are satisfied for the same patch. For example, when the log-fecundities  $\log a_t^i(r)$  are independent and normally distributed with mean  $\mu_i(r)$  and variance  $\sigma_i^2(r)$ , the coexistence conditions become

$$\mu_2(r) - \mu_1(r) + \frac{\sigma_1^2(r) + \sigma_2^2(r)}{2} > 1$$

for some patch  $r$  and

$$\mu_1(s) - \mu_2(s) + \frac{\sigma_1^2(s) + \sigma_2^2(s)}{2} > 1$$

for some patch  $s$ . Both conditions can be satisfied in the same patch  $r$  provided that  $\sigma_1(r)$  or  $\sigma_2(r)$  are sufficiently large.

**Biological Interpretation 6.1.** *For relatively sedentary populations, coexistence occurs if each species has a patch it can invade when rare. If the populations are also short-lived, coexistence requires that each species has a patch in which it is competitively dominant. Alternatively, if populations are long-lived, regional coexistence may occur if species coexist locally within a patch due to the storage effect. For uncorrelated and log-normally distributed fecundities, this within-patch storage effect occurs if the difference in the mean log-fecundities is sufficiently smaller than the net variance in the log-fecundities.*

**6.3. Well-mixed populations.** For populations that are highly dispersive (i.e.  $d = \frac{m-1}{m}$ ), the spatially explicit Lottery model reduces to a spatially implicit model where

$$\begin{aligned} r_1(\delta_2) &= \mathbb{E} \left[ \log \left( \varepsilon \frac{\sum_r \xi_t^1(r)}{\sum_r \xi_t^2(r)} + 1 - \varepsilon \right) \right] \text{ and} \\ r_2(\delta_1) &= \mathbb{E} \left[ \log \left( \varepsilon \frac{\sum_r \xi_t^2(r)}{\sum_r \xi_t^1(r)} + 1 - \varepsilon \right) \right]. \end{aligned}$$

For short lived populations ( $\varepsilon = 1$ ), these long-term growth rates simplify to

$$\begin{aligned} r_1(\delta_2) &= \mathbb{E} \left[ \log \sum_r \xi_t^1(r) \right] - \mathbb{E} \left[ \log \sum_r \xi_t^2(r) \right] \\ r_2(\delta_1) &= \mathbb{E} \left[ \log \sum_r \xi_t^2(r) \right] - \mathbb{E} \left[ \log \sum_r \xi_t^1(r) \right] \end{aligned}$$

Since  $r_1(\delta_2) = -r_2(\delta_1)$ , the persistence criterion that  $r_1(\delta_2) > 0$  and  $r_2(\delta_1) > 0$  is not satisfied generically.

Alternatively, for long-lived populations ( $\varepsilon \approx 0$ ), the invasion rates of well-mixed populations becomes to first-order in  $\varepsilon > 0$ :

$$\begin{aligned} r_1(\delta_2) &\approx \varepsilon \left( \mathbb{E} \left[ \frac{\sum_r \xi_t^1(r)}{\sum_r \xi_t^2(r)} \right] - 1 \right) \\ r_2(\delta_1) &\approx \varepsilon \left( \mathbb{E} \left[ \frac{\sum_r \xi_t^2(r)}{\sum_r \xi_t^1(r)} \right] - 1 \right) \end{aligned}$$

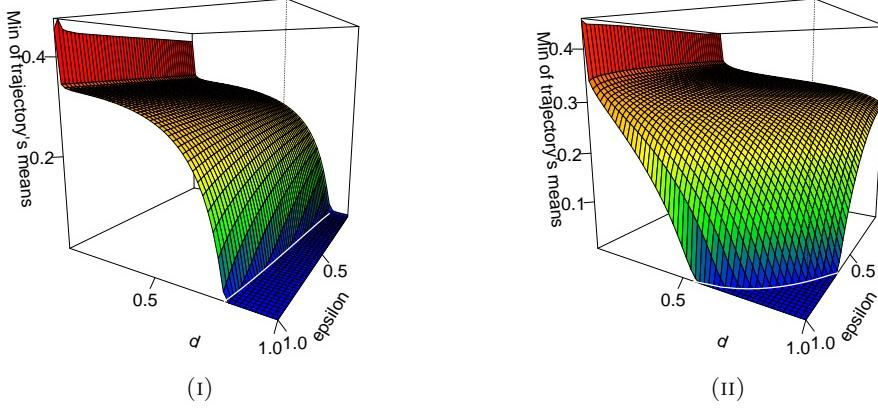


FIGURE 3. Effects of dispersal and survival on coexistence of two species. The log-fecundities  $\xi^i$  are independent and normally distributed with means  $\mu_1 = (5, 0, 5, 0, \dots, 0)$ ,  $\mu_2 = (0, 5, 0, \dots, 0)$  and variances  $\sigma_1^2 = \sigma_2^2 = (1, \dots, 1)$  for (I) and  $(3, \dots, 3)$  for (II). The white lines correspond to the zero-lines of the respective Lyapunov exponents.

We conjecture that this coexistence condition is less likely to be met than the coexistence condition for relatively sedentary populations. To see why, we perform a small variance approximation of these invasion rates. Assume that  $\xi_t^i = \bar{\xi}^i + \varepsilon Z_t^i(r)$  where  $Z_t^i(r)$  are independent and identically distributed in  $i, r$  and  $\mathbb{E}[Z_t^i(r)] = 0$  for all  $i, r$ . Let  $\sigma^2 = \mathbb{E}[(Z_t^i(r))^2]$ . A second order Taylor's approximation in  $\varepsilon$  yields the following approximation of the (rescaled) long-term growth rates for well-mixed populations

$$(18) \quad \mathbb{E} \left[ \frac{\sum_r \xi_t^1(r)}{\sum_r \xi_t^2(r)} \right] - 1 \approx \frac{\bar{\xi}^1}{\bar{\xi}^2} + \frac{\bar{\xi}^1 \sigma^2 / n}{(\bar{\xi}^2)^3} - 1$$

and the following approximation for relatively sedentary populations

$$(19) \quad \max_r \mathbb{E} \left[ \frac{\xi_t^1(r)}{\xi_t^2(r)} \right] - 1 \approx \frac{\bar{\xi}^1}{\bar{\xi}^2} + \frac{\bar{\xi}^1 \sigma^2}{(\bar{\xi}^2)^3} - 1$$

Since (19) is greater than (18), persistence is more likely for relatively sedentary populations in this small noise limit.

**Biological Interpretation 6.2.** *Short-lived and highly dispersive competitors do not satisfy the coexistence condition. Long-lived and highly-dispersive competitors may coexist. However, coexistence appears to be less likely than for sedentary populations as spatial averaging reduces the temporal variability experienced by both populations and, thereby, weakens the storage effect.*

**6.4. The rock-paper-scissor game.** In the last few years the rock-paper-scissor game, which might initially seem to be of purely theoretical interest, has emerged as playing an important role in describing the behavior of various real-world systems. These include the evolution of alternative male mating strategies in the side-blotted lizard *Uta stansburiana* [Sinervo and Lively, 1996], the *in vitro* evolution of bacterial populations [Kerr et al., 2002, Nahum et al., 2011], the *in vivo* evolution of bacterial populations in mice [Kirkup and Riley, 2004], and the competition between

genotypes and species in plant communities [Lankau and Strauss, 2007, Cameron et al., 2009]. More generally, the rock-scissors-paper game – which is characterized by three strategies R, P and S, which satisfy the non-transitive relations: P beats R (in the absence of S), S beats P (in the absence of R), and R beats S (in the absence of P) – serves as a simple prototype for studying the dynamics of more complicated non-transitive systems [Buss and Jackson, 1979, Paquin and Adams, 1983, May and Leonard, 1975, Schreiber, 1997, Schreiber and Rittenhouse, 2004, Vandermeer and Pascual, 2005, Allesina and Levine, 2011]. Here, we examine a simple spatial version of this evolutionary game in a fluctuating environment.

Let  $x_t^1(r)$ ,  $x_t^2(r)$ , and  $x_t^3(r)$  be the frequencies of the rock, paper, and scissor strategies in patch  $r$ , respectively. All strategies in patch  $r$  receive a basal payoff of  $a_t^r$  at time  $t$ . Winners in an interaction in patch  $r$  receive a payoff of  $b_t^r$  while losers pay a cost  $c_t^r$ . Thus, the payoff matrix for the interacting populations in patch  $r$  is

$$\Xi_t(r) = a_t^r + \begin{pmatrix} 0 & -c_t^r & b_t^r \\ b_t^r & 0 & -c_t^r \\ -c_t^r & b_t^r & 0 \end{pmatrix}.$$

We continue to assume that the fraction of progeny dispersing from patch  $r$  to patch  $s$  equals  $d/(m-1)$  for  $s \neq r$  and  $1-d$  otherwise.

Our first result about the rock-paper-scissor model is that it exhibits a heteroclinic cycle in  $S_0$  between the three equilibria  $E_1 = (1, \dots, 1, 0, \dots, 0, 0, \dots, 0)$ ,  $E_2 = (0, \dots, 0, 1, \dots, 1, 0, \dots, 0)$  and  $E_3 = (0, \dots, 0, 0, \dots, 0, 1, \dots, 1)$ .

**Proposition 6.3.** *Assume  $d, \varepsilon \in (0, 1]$  and  $a_t^r > c_t^r$ ,  $\log a_t^r, \log c_t^r, \log b_t^r \in [-M, M]$  with probability one for some  $M > 0$ . If  $x_0^1 > (0, \dots, 0)$  and  $x_0^2 > (0, \dots, 0)$  and  $x_0^3 = (0, \dots, 0)$ , then  $\lim_{t \rightarrow \infty} x_t = E_2$  with probability one. If  $x_0^1 > (0, \dots, 0)$  and  $x_0^3 > (0, \dots, 0)$  and  $x_0^2 = (0, \dots, 0)$ , then  $\lim_{t \rightarrow \infty} x_t = E_1$  with probability one. If  $x_0^2 > (0, \dots, 0)$  and  $x_0^3 > (0, \dots, 0)$  and  $x_0^1 = (0, \dots, 0)$ , then  $\lim_{t \rightarrow \infty} x_t = E_3$  with probability one.*

*Proof.* It suffices to prove the assertion for the case in which  $x_0^1 > (0, \dots, 0)$  and  $x_0^2 > (0, \dots, 0)$  and  $x_0^3 = (0, \dots, 0)$ . Let  $\mathbf{1} = (1, \dots, 1) \in \mathbb{R}^n$ . Our assumptions  $b_t^r > 0$  and  $a_t^r > c_t^r > 0$  imply there exists  $\eta > 0$  such that  $\Xi^2(\xi_{t+1}, X_t) \gg \exp(\eta) \Xi^1(\xi_{t+1}, X_t)$  with probability one. It follows that

$$\begin{aligned} \limsup_{t \rightarrow \infty} \frac{1}{t} \log \|X_t^1\| &= \limsup_{t \rightarrow \infty} \frac{1}{t} \log \|\Xi^1(\xi_t, X_{t-1}) \dots \Xi^1(\xi_1, X_0) X_0^1\| \\ &\leq \limsup_{t \rightarrow \infty} \frac{1}{t} \log \|\Xi^2(\xi_t, X_{t-1}) \dots \Xi^2(\xi_1, X_0) X_0^1\| - \eta \\ &= \limsup_{t \rightarrow \infty} \frac{1}{t} \log \|\Xi^2(\xi_t, X_{t-1}) \dots \Xi^2(\xi_1, X_0) X_0^2\| - \eta \\ &\leq -\eta \end{aligned}$$

where the last two lines follow from Proposition 8.14 and its Corollary. Hence,  $\lim_{t \rightarrow \infty} \|X_t^1\| = 0$  as claimed.  $\square$

Proposition 6.3 implies that all invariant measures on  $S_0$  are given by convex combinations of Dirac measures at the pure strategy equilibria. More specifically, define  $\delta_i$  to be the Dirac measure concentrated at the pure-strategy  $i$  equilibrium. Any invariant measure  $\nu$  on  $S_0$  is given by  $\sum_i p_i \delta_i$  for a probability vector  $p =$

$(p_1, p_2, p_3)$ . The persistence criterion of Theorem 3.4 requires that

$$\min_{p \in \Delta_3} \max_{j \in \{1, 2, 3\}} \sum_i p_i r_j(\delta_i) > 0$$

where  $\Delta_3 = \{p \in \mathbb{R}_+^3 : p_1 + p_2 + p_3 = 1\}$  the simplex of probability vectors. A standard algebraic calculation shows that this persistence criterion is satisfied if and only if

$$r_2(\delta_1)r_3(\delta_2)r_1(\delta_3) > -r_3(\delta_1)r_1(\delta_2)r_2(\delta_3)$$

i.e. the product of the positive invasion rates is greater than the absolute value of the product of the negative invasion rates. The symmetry of our model implies that all the positive invasion rates are equal and all the negative invasion rates are equal. Hence, coexistence requires

$$r_3(\delta_2) > -r_1(\delta_1)$$

As we did for the case of two competing species, we can derive more explicit coexistence criteria when the populations relatively sedentary (i.e.  $d \approx 0$ ) or the populations are well-mixed (i.e.  $d = 1$ ). For relatively sedentary populations, the coexistence criterion becomes

$$\max_r \mathbb{E} \left[ \log \left( 1 - \varepsilon + \varepsilon \frac{a_t^r + b_t^r}{a_t^r} \right) \right] > - \max_r \mathbb{E} \left[ \log \left( 1 - \varepsilon + \varepsilon \frac{a_t^r - c_t^r}{a_t^r} \right) \right]$$

For long-lived populations, this coexistence criterion simplifies further to

$$\max_r \mathbb{E} \left[ \frac{b_t^r}{a_t^r} \right] > \min_r \mathbb{E} \left[ \frac{c_t^r}{a_t^r} \right]$$

Alternatively, when the populations are well-mixed, the coexistence criterion becomes

$$\mathbb{E} \left[ \log \left( 1 - \varepsilon + \varepsilon \frac{\sum_r a_t^r + b_t^r}{\sum_r a_t^r} \right) \right] > - \max_r \mathbb{E} \left[ \log \left( 1 - \varepsilon + \varepsilon \frac{\sum_r a_t^r - c_t^r}{\sum_r a_t^r} \right) \right]$$

For long-lived populations, this coexistence criterion simplifies further to

$$\mathbb{E} \left[ \frac{\sum_r b_t^r}{\sum_r a_t^r} \right] > \min_r \mathbb{E} \left[ \frac{\sum_r c_t^r}{\sum_r a_t^r} \right]$$

**Biological Interpretation 6.4.** *For relatively sedentary populations, coexistence only requires that average benefits (relative to the base payoff) in one patch is greater than the average costs (relative to the base payoff) in another patch. Negative correlations between benefits  $b_t^r$  and basal payoffs  $a_t^r$  promote coexistence. For highly dispersive species, If base payoffs are constant in space in time (i.e.  $a_t^r = a$  for all  $t, r$ ), then coexistence requires the spatially and temporally averaged benefits of interactions exceed the spatially and temporally averaged costs of interactions.*

## 7. DISCUSSION

Understanding the conditions that ensure the long-term persistence of interacting populations is of fundamental theoretical and practical importance in population biology. For deterministic models, coexistence naturally corresponds to an attractor bounded away from extinction. Since populations often experience large perturbation, many authors have argued that the existence of a global attractor (i.e. permanence or uniform persistence) may be necessary for long-term persistence [Hofbauer and Sigmund, 1998, Smith and Thieme, 2011]. Most populations experience stochastic fluctuations in their demographic parameters [May, 1973] which raises the

question [May, 1973, pg.621] “How are the various usages of the term [persistence] in deterministic and stochastic circumstances related?” Only recently has it been shown that the deterministic criteria for permanence extend naturally to criteria for stochastic persistence in stochastic difference and differential equations [Benaïm et al., 2008, Schreiber et al., 2011]. These criteria assume that the populations are unstructured (i.e. no differences among individuals) and environmental fluctuations are temporally uncorrelated. However, many populations are structured as highlighted in a recent special issue in *Theoretical Population Biology* [Tuljapurkar et al., 2012] devoted to this topic. Moreover, many environmental factors such as temperature and precipitation exhibit temporal autocorrelations [Vasseur and Yodzis, 2004]. Here, we prove that by using long-term growth rates when rare, the standard criteria for persistence extend to models of interacting populations experiencing correlated as well as uncorrelated environmental stochasticity, exhibiting within population structure, and any form of density-dependent feedbacks. To illustrate the utility of these criteria, we applied them to persistence of predator-prey interactions in auto-correlated environments, structured populations with over-compensating density-dependence, and competitors in spatially structured environments.

Mandelbrot [1982] proposed that environmental signals commonly found in nature may be composed of frequencies  $f$  that scale according to an inverse power law  $1/f^\beta$ . With this scaling, uncorrelated (i.e. white) noise corresponds to  $\beta = 0$ , positively auto-correlated (i.e. red or brown) noise corresponds to  $\beta > 0$ , and negatively auto-correlated (e.g. blue) noise corresponds to  $\beta < 0$ . Many environmental signals important to ecological processes including precipitation, mean air temperature, degree days, and seasonal indices exhibit positive  $\beta$  exponents [Vasseur and Yodzis, 2004]. Consistent with prior work on models with compensating density dependence [Roughgarden, 1975, Johst and Wissel, 1997, Petchey, 2000], we found that positive autocorrelations in the maximal per-capita growth rate of species increases the long-term variability in their densities. If this species is the prey for a predatory species, we showed that this increased variability in prey densities reduced a predator’s realized per-capita growth rate when rare. Hence, positive autocorrelations may impede predator-prey coexistence. In contrast, negative autocorrelations, possibly due to a biotic feedback between the prey species and its resources, may facilitate coexistence by reducing variation in prey densities and, thereby, increase the predator’s growth rate when rare. These results are qualitatively consistent with prior results that positive-autocorrelations in predator-prey systems can increase variation in prey and predator densities when they coexist [Collie and Spencer, 1994, Ripa and Ives, 2003]. Specifically, in a simulation study of predator-prey interactions in pelagic fish stocks, Collie and Spencer [1994] found reddened noise resulted in predator-prey densities “to shift between high and low equilibrium levels” and, thereby, increase variability in their abundances. Similarly, using linear approximations, Ripa and Ives [2003] found that environmental autocorrelations increased the amplitude of populations cycles.

Classical stochastic demography theory [Tuljapurkar, 1990, Boyce et al., 2006] considers population growth rates in the absence of density-dependent feedbacks. Our results for populations experiencing negative-density dependence show that stochastic persistence depends on the population’s long-term growth rate  $r(0)$  when rare. Hence, applying stochastic demography theory to  $r(0)$  provides insights into how environmental stochasticity interacts with population structure to determine

stochastic persistence. For example, a fundamental result from stochastic demography is that positive, within-year correlations between vital rates decreases  $r(0)$  and thereby may thwart stochastic persistence, a result consistent with our analysis of the stochastic LPA model for flour beetle dynamics. Stochastic demography theory also highlights that temporal autocorrelations can have subtle effects on  $r(0)$ . In particular, for a density-independent version of the metapopulation model considered here, Schreiber [2010] demonstrated that positive temporal autocorrelations can increase the metapopulation growth rate  $r(0)$  when rare for partially mixing populations, a prediction consistent with laboratory experiments [Matthews and Gonzalez, 2007]. In contrast, Tuljapurkar and Haridas [2006] found that negative temporal autocorrelations between years with and without fires increased the realized per-capita growth rate  $r(0)$  for models of the endangered herbaceous perennial *Lomatium bradshawii*.

Spatial heterogeneity of populations has been shown theoretically and empirically to have an effect on coexistence of competitive species (see e.g. Amarasekare [2003] or Chesson [2000b] for a review). Coexistence requires species to exhibit niche differentiation that decrease the interspecific competition [Chesson, 2000a]. In a fluctuating environment, these niches can arise as differential responses to temporal variation [McGehee and Armstrong, 1977, Armstrong and McGehee, 1980, Chesson, 2000a,b], spatial variation [May and Hassell, 1981, Chesson, 2000a,b], or a combination of both forms of variation [Chesson, 1985]. For the spatial lottery model where species disperse between a finite number of patches and compete for micro sites within these patches, our coexistence criterion applies, and reduces to the *mutual invisibility* criterion. Although Chesson [1985] proved this result in the limit of an infinite number of patches with temporally uncorrelated fluctuations, our result is less restrictive as the number of patches can be small and temporal fluctuations can be autocorrelated. Using this mutual invisibility criterion, we derive explicit coexistence criteria for relatively sedentary populations and highly dispersive populations. In the former case, coexistence occurs if each species has a patch it can invade when rare. For short-lived populations, coexistence requires that each species has a patch in which it is competitively dominant. Alternatively, for long-lived populations, regional coexistence may occur if species coexist locally within a patch due to the storage effect [Chesson and Warner, 1981, Chesson, 1982, 1994] in the *one patch* case. For highly dispersive populations, the coexistence criterion is only satisfied if populations exhibit overlapping generations, a conclusion consistent with [Chesson, 1985]. By providing the first mathematical confirmation of the mutual invisibility criterion for the spatial lottery model with spatial and temporal variation, our result opens the door for deeper investigations in understanding the relative roles of temporal variation, spatial heterogeneity, and dispersal on coexistence. Such investigations could extend the work of Chesson [1985] and Muko and Iwasa [2000] who showed that, without environmental variation, *between-patch* variation in the ratio of mortalities of two species promotes coexistence, while that of reproductive rates does not.

For lottery models with three or more species, persistence criteria are more subtle and invasibility of all sub communities isn't always sufficient [May and Leonard, 1975]. For example, in rock-paper-scissor communities where species 2 displaces species 1, 3 displaces 2, and 1 displaces 3, all sub communities which consist of a single species are invisible by another, but coexistence may not occur [Hofbauer and Sigmund, 1998, Schreiber and Killingback, in press]. For the deterministic models, coexistence requires that the geometric mean of the benefits of pair-wise

interactions exceeds the costs of these interactions [Schreiber and Killingback, in press]. Schreiber et al. [2011] and Schreiber and Killingback [in press] studied these interactions in models *separately* accounting for temporal fluctuations or spatial heterogeneity. In both cases, temporal heterogeneity or spatial heterogeneity can individually promote coexistence. Here we extend these result to intransitive communities experiencing both spatial heterogeneity and temporal fluctuations, thereby unifying this prior work. Our persistence criterion reduces to: the geometric mean of the positive long-term, low-density growth rates of each species (e.g. invasion rate of rock to scissor) is greater than the geometric mean of the absolute values of the negative, long-term, low-density growth rates (e.g. invasion rate of rock to paper). For relatively sedentary populations, coexistence only requires that average benefits (relative to the base payoff) in one patch is greater than the average costs in another patch. Moreover, negative correlations between benefits and basal payoffs promote coexistence. For highly dispersive species, coexistence requires the spatially and temporally averaged benefits of interactions exceed the spatially and temporally averaged costs of interactions, assuming that base payoffs are constant in space and time.

The theory of stochastic population dynamics is confronted with many, exciting challenges. While we have provided a sufficient condition for stochastic persistence, it is equally important to develop sufficient conditions for the asymptotic exclusion of one or more species with positive probability. In light of the deterministic theory, a natural conjecture in this direction is the following: if there exist non-negative weights  $p_1, \dots, p_k$  such that

$$\sum_i p_i r_i(\mu) < 0$$

for every ergodic measure  $\mu$  supported on the extinction set  $S_0$ , then there exist positive initial conditions such that  $X_t$  asymptotically approaches  $S_0$  with positive probability. Benaïm et al. [2008] proved a stronger version of this conjecture for stochastic differential equation models where the diffusion term is small and the populations are unstructured. However, it is not clear whether these methods carry over to models with “large” noise or population structure. Another important challenge is relaxing the compactness assumption **H4** for our stochastic persistence results. While this assumption is biologically realistic (i.e. populations always have an upper limit on their size), it is theoretically inconvenient as many natural models of environmental noise have non-compact distributions (e.g. log-normal or gamma distributions). One promising approach developed by Benaïm and Schreiber [2009] for structured models of single species is identifying Lyapunov-like functions that decrease on average when population densities get large. Finding sufficient conditions for “stochastic boundedness” is only half of the challenge, extending the stochastic persistent results to these “stochastically bounded” models will require additional innovations. Finally, and most importantly, there is a desperate need to develop more tools to analytically approximate or directly compute the long-term growth rates  $r_i(\mu)$  when rare.

## 8. PROOF OF THEOREMS 3.1 AND 3.4

Most of this Appendix is devoted to the proof of Theorem 3.4 from which Theorem 3.1 follows. In section 8.1, we recast our stochastic model (1) and our main hypothesis in Arnold’s framework of random dynamical system [Arnold, 1998]. Since

the dynamics we consider may not be invertible, in section 8.2 we extend the dynamics to a dynamics on the set of possible trajectories to get an invertible dynamic on a larger space. Then we state Theorem 8.10 from which Theorem 3.4 follows. In section 8.3, we prove basic results about the average per-capita growth rates  $r_i$ . In section 8.4, we prove several basic results about occupational measures and their weak\* limit points. A proof of Theorem 8.10 is provided in section 8.5. The proofs of Theorems 3.1 and 3.4 follows as a corollary of Theorem 8.10 (see Remark 8.11).

**8.1. Random dynamical systems framework .** To prove our main result, it is useful to embed (1) and assumptions **H1-H4** within Arnold's general framework of random dynamical systems (Arnold [1998]). Let  $\Omega = E^{\mathbb{Z}}$  be the set of possible environmental trajectories,  $\mathcal{F} = \mathcal{E}^{\mathbb{Z}}$  be the product  $\sigma$ -algebra on  $\Omega$ ,  $\theta : \Omega \mapsto \Omega$  be the shift operator defined by  $\theta(\{\omega_t\}_{t \in \mathbb{Z}}) = \{\omega_{t+1}\}_{t \in \mathbb{Z}}$ , and  $\mathbb{Q}$  be the probability measure on  $\Omega$  satisfying

$$\mathbb{Q}(\{\omega \in \Omega : \omega_t \in E_0, \dots, \omega_{t+k} \in E_k\}) = \mathbb{P}(\xi_0 \in E_0, \dots, \xi_k \in E_k)$$

for any Borel sets  $E_0, \dots, E_n \subset E$ . Since  $E$  is a Polish space, the space  $\Omega$  endowed with the product topology is Polish as well. Therefore, by the Kolmogorov consistency theorem, the probability measure  $\mathbb{Q}$  is well defined, and by a theorem of Rokhlin [1964],  $\theta$  is ergodic with respect to  $\mathbb{Q}$ . Randomness enters by choosing randomly a point  $\omega = \{\omega_t\}_{t \in \mathbb{Z}} \in \Omega$  with respect to the probability distribution  $\mathbb{Q}$  and defining the environmental state at time  $t$  by  $\omega_t$ .

In this framework, the dynamics (1) takes on the form

$$(20) \quad \begin{cases} X_{t+1}(\omega, x) = X_t(\omega, x)A(\omega_t, X_t(\omega, x)) \\ X_0(\omega, x) = x \in S. \end{cases}$$

We call (20), the *random dynamical system determined by  $(\theta, \mathbb{P}, A)$* .

To state the assumptions in this framework, define the skew product  $\Phi : \Omega \times \mathbb{R}_+^n \rightarrow \Omega \times \mathbb{R}_+^n$  associated with the dynamics (20) by

$$\Phi(\omega, x) := (\theta(\omega), xA(\omega_0, x)),$$

and the projection maps  $p_1 : \Omega \times \mathbb{R}^n \rightarrow \Omega$  and  $p_2 : \Omega \times \mathbb{R}^n \rightarrow \mathbb{R}^n$  by  $p_1(x, \omega) = \omega$  and  $p_2(x, \omega) = x$ .

**Definition 8.1.** A compact set  $K \subset \Omega \times \mathbb{R}_+^n$  is a global attractor for  $\Phi$  if there exists a neighborhood  $V$  of  $K$  such that

- (i) for all  $(\omega, x) \in \Omega \times \mathbb{R}_+^n$ , there exist  $T \geq 0$  such that  $\Phi^t(\omega, x) \in V$  for all  $t \geq T$ ;
- (ii)  $\Phi(V) \subset V$  and  $K = \bigcap_{t \in \mathbb{N}} \Phi^t(V)$ .

Assumptions **H3-H4** take on the form

**H3'**: There exists a global attractor  $K \subset \Omega \times \mathbb{R}_+^n$  for  $\Phi$ .

**H4'**:  $\Omega$  is a compact space,  $\mathbb{Q}$  is a Borel probability measure, and  $\theta$  is an invertible map that is ergodic with respect to  $\mathbb{Q}$ , i.e. for all Borel set  $B \subset \Omega$ , such that  $\theta^{-1}(B) = B$ , we have  $\mathbb{Q}(B) \in \{0, 1\}$ .

Assumptions **H1-H2** do not need to be rewritten in the new framework. Assumption **H3'** is simply restatement of assumption **H3** in the random dynamical systems framework. Since every ergodic stationary processes on a Polish space can be described as an ergodic measure preserving transformation (Kolmogorov consistency theorem and Rokhlin theorem), assumption **H4'** is less restrictive than **H4**.

To state Theorem 3.4 in this more general framework, we define *invariant measures for the random dynamical system* (20). We follow the definition given by Arnold [1998]. First, recall some useful definitions and notations. We define  $\text{int } \mathbb{R}_+^d := \{x \in \mathbb{R}_+^d : \prod_i x_i > 0\}$  and  $\mathbf{M}_d(\mathbb{R})$  the set of all  $d \times d$  matrices over  $\mathbb{R}$ . Let  $M$  be a metric space, and let  $\mathcal{P}(M)$  be the space of Borel probability measures on  $M$  endowed with the weak\* topology. If  $M'$  is also a metric space and  $f: M \rightarrow M'$  is Borel measurable, then the induced linear map  $f^*: \mathcal{P}(M) \rightarrow \mathcal{P}(M')$  associates with  $\nu \in \mathcal{P}(M)$  the measure  $f^*(\nu) \in \mathcal{P}(M')$  defined by

$$f^*(\nu)(B) = \nu(f^{-1}(B))$$

for all Borel sets  $B$  in  $M'$ . If  $\theta: M \rightarrow M$  is a continuous map, a measure  $\nu \in \mathcal{P}(M)$  is called  $\theta$ -*invariant* if  $\nu(\theta^{-1}(B)) = \nu(B)$  for all Borel sets  $B \in M$ . A set  $B \subset M$  is *positively invariant* if  $\theta(B) \subset B$ . For every positively invariant compact set  $B$ , we call  $\text{Inv}(\theta)(B)$  the set of all  $\theta$ -invariant measures supported on  $B$ .

**Definition 8.2.** A probability measure  $\mu$  on  $\Omega \times \mathbb{R}_+^n$  is *invariant* for the random dynamical system (20) if

- (i)  $\mu \in \text{Inv}(\Phi)$ ,
- (ii)  $p_1^*(\mu) = \mathbb{Q}$ , i.e. for all Borel sets  $D \subset \Omega$ ,  $\mu(D \times \mathbb{R}_+^n) = \mathbb{Q}(D)$ .

For any positively invariant set  $\Omega \times C$  where  $C \subset \mathbb{R}_+^n$  is compact,  $\text{Inv}_{\mathbb{Q}}(\Phi)(\Omega \times C)$  is the set of all measures  $\mu$  satisfying (i) and (ii) such that  $\mu(\Omega \times C) = 1$ .

**Remark 8.3.** There is a bijection between the set of measures defined in Definition 3.2 and the set  $\text{Inv}_{\mathbb{Q}}(\Phi)(\Omega \times \mathbb{R}_+^n)$ .

The following result is a consequence of Theorem 1.5.10 in Arnold [1998]. In fact, the topology defined in his definition 1.5.3 is finer than the weak\* topology on the set of all probability measures on  $\Omega \times C$ .

**Proposition 8.4.** If  $C \subset \mathbb{R}_+^n$  is a positively invariant compact set, then  $\text{Inv}_{\mathbb{Q}}(\Phi)(\Omega \times C)$  is a nonempty, convex, compact subset  $\mathcal{P}(\Omega \times \mathbb{R}_+^n)$ .

The main assumption in Theorem 3.4 deals with the long-term growth rates which characterize, in some sense, the long term behavior of random matrix products (see Definition 3.3). In order to define those products in the new framework, we consider the maps  $A_i: \Omega \times S \rightarrow \mathbf{M}_{n_i}(\mathbb{R})$  defined by

$$A_i(\omega, x) = A_i(\omega_0, x).$$

While our choice of notation here differs slightly from the main text, this choice simplifies the proof. We write

$$(21) \quad A_i^t(\omega, x) := A_i(\omega, x)A_i(\Phi(\omega, x)) \cdots A_i(\Phi^{t-1}(\omega, x)),$$

with the convention that  $A_i^0(\omega, x) = \text{id}$ , the identity matrix.

Then, for each  $i \in \{1, \dots, m\}$ , the asymptotic growth rate of the product (21) associated with  $(\omega, x) \in \Omega \times \mathbb{R}_+^n$  is

$$r_i(x, \omega) := \limsup_{t \rightarrow \infty} \frac{1}{t} \ln \|A_i^t(\omega, x)\|,$$

which is finite due to assumption **H1**. According to Definition 8.2, the *invasion rate of species  $i$  with respect to an invariant measure  $\mu \in \text{Inv}_{\mathbb{Q}}(\Phi)$*  is

$$r_i(\mu) := \int_{\Omega \times \mathbb{R}_+^n} r_i(\omega, x) \mu(d\omega, dx).$$

Given a point  $(\omega, x) \in \Omega \times \mathbb{R}_+^n$ , let  $\Pi_t(\omega, x)$  denote the empirical occupation measure of the process of (20) at time  $t$  defined by

$$\Pi_t(\omega, x) := \frac{1}{t} \sum_{s=0}^{t-1} \delta_{X_s(\omega, x)}.$$

For each Borel set  $B \subset \mathbb{R}_+^n$ , the random variable  $\Pi_t^x(B)$  given by (2) is equal in distribution to the random variable  $\Pi_t(\cdot, x)(B)$ .

For all  $\eta > 0$ , recall that  $S_\eta := \{x \in \mathbb{R}_+^n : \|x^i\| \leq \eta \text{ for some } i\}$ . We can now rephrase Theorem 3.4 in the framework of random dynamical systems.

**Theorem 8.5.** *If one of the following equivalent conditions hold*

- (i)  $r_*(\mu) := \max_{0 \leq i \leq m} r_i(\mu) > 0$  for every probability measure  $\mu \in \text{Inv}_{\mathbb{Q}}(\Phi)(\Omega \times S_0)$ , or
- (ii) there exist positive constants  $p_1, \dots, p_m$  such that

$$\sum_i p_i r_i(\mu) > 0$$

for every ergodic probability measure  $\mu \in \text{Inv}_{\mathbb{Q}}(\Phi)(\Omega \times S_0)$ , or

- (iii) there exist positive constants  $p_1, \dots, p_m$  such that

$$\sum_i p_i r_i(\omega, x) > 0$$

for every  $x \in S_0$  and  $\mathbb{Q}$ -almost all  $\omega \in \Omega$ ,

then for all  $\varepsilon > 0$ , there exists  $\eta > 0$  such that

$$\limsup_{t \rightarrow \infty} \Pi_t(\omega, x)(S_\eta) \leq \varepsilon \quad \text{for } \mathbb{Q}\text{-almost all } \omega,$$

whenever  $x \in \mathbb{R}_+^n \setminus S_0$ .

**8.2. Trajectory space.** The key element of the proof of Theorem 8.5 is Proposition 8.13 due to Ruelle [1979b] in which it is crucial that dynamics induced by  $\Phi$  is an homeomorphism. For now, it is not the case. Indeed, the map  $\Phi$  is, a priori, not invertible. The aim of this subsection is to extend the dynamics induced by  $\Phi$  to an invertible dynamics on the larger set of possible trajectories. Then, we state an equivalent version of Theorem 8.5 in this larger space.

By definition of the global attractor  $K$ , there exist a neighborhood  $V$  of  $p_2(K)$  in  $\mathbb{R}_+^n$  such that  $\Phi(\Omega \times V) \subset \Omega \times V$ . By continuity of  $\Phi$ , this inclusion still holds for the closure  $\overline{V}$  of  $V$ , i.e.

$$\Phi(\Omega \times \overline{V}) \subset \Omega \times \overline{V}.$$

This inclusion implies that, for every point  $(\omega, x) \in \Omega \times \overline{V}$ , there exists a sequence  $\{(\omega_t, x_t)\}_{t \in \mathbb{N}} \subset (\Omega \times \overline{V})^{\mathbb{N}}$  such that  $(\omega_0, x_0) = (\omega, x)$ , and  $(\omega_{t+1}, x_{t+1}) = \Phi(\omega_t, x_t)$  for all  $t \geq 0$ . Such a sequence is called a  *$\Phi$ -positive trajectory*. In order to create a *past* for all those  $\Phi$ -positive trajectories, let us pick a point  $(\omega^*, x^*) \in \Omega \times S \setminus \overline{V}$ , and consider the sequence space  $\mathcal{T} := (\Omega \times \overline{V} \cup \{x^*\})^{\mathbb{Z}}$  endowed with the product topology, and the *shift operator*  $\Theta : \mathcal{T} \rightarrow \mathcal{T}$  defined by  $\Theta(\{(\omega_t, x_t)\}_{t \in \mathbb{Z}}) = \{(\omega_{t+1}, x_{t+1})\}_{t \in \mathbb{Z}}$ . Since both  $\Omega$  and  $\overline{V} \cup \{x^*\}$  are compact, the space  $\mathcal{T}$  is compact as well.

Define

$$\Gamma = \{(\omega_t, x_t)\}_{t \in \mathbb{Z}} \in \mathcal{T} : (\omega_{t+1}, x_{t+1}) = \Phi(\omega_t, x_t), \quad \text{whenever } x_t \in \overline{V},$$

endowed with the induced topology. Every  $\Phi$ -positive solution can be seen as an element of  $\mathcal{T}$  by creating a fixed past (i.e.  $(\omega_t, x_t) = (\omega^*, x^*)$  for all  $t < 0$ ). Then  $\Gamma$  is

the union of  $(\Omega \times \{x^*\})^{\mathbb{Z}}$  and of the adherence of the set of all shifted (by  $\Theta^t$  for some  $t \in \mathbb{Z}$ )  $\Phi$ -positive solutions. Since  $\Gamma$  is a closed subset of the compact  $\mathcal{T}$ , it is compact as well. Moreover  $\Gamma$  is invariant under  $\Theta$ , which implies that the restriction  $\Theta|_{\Gamma}$  of  $\Theta$  on  $\Gamma$  is well-defined. To simplify the presentation we still denote this restriction by  $\Theta$ . The projection map  $\pi_0 : \Gamma \rightarrow \Omega \times \overline{V} \cup \{x^*\}$  is defined by  $\pi_0(\gamma) = (\omega_0, x_0)$  for all  $\gamma = \{(\omega_t, x_t)\}_{t \in \mathbb{Z}} \in \Gamma$ . By definition, the map  $\pi_0$  is continuous and surjective. For now on, when we write  $\gamma \in \Gamma$ , we mean  $\gamma = \{(\omega_t, x_t)\}_{t \in \mathbb{Z}}$ .

Next, we define the compact set of all  $\Phi$ -total trajectories as

$$\Gamma_+ := \pi_0^{-1}(\Omega \times \overline{V}),$$

and the compact set of  $\Phi$ -total-solution trajectory on the extinction set  $S_0$  as

$$\Gamma_0 := \pi_0^{-1}(\Omega \times S_0).$$

The dynamic induced by  $\Phi$  on  $\Omega \times \overline{V}$  is linked to the dynamic induced by  $\Theta$  on  $\Gamma_+$  by the following semi conjugacy

$$(22) \quad \pi_0 \circ \Theta = \Phi \circ \pi_0.$$

For  $B \subset \Gamma$  positively invariant and compact, define

$$\text{Inv}_{\mathbb{Q}}(\Theta)(B) := \{\tilde{\mu} \in \text{Inv}(\Theta)(B) : p_1^* \circ \pi_0^*(\tilde{\mu}) = \mathbb{Q}\}.$$

**Proposition 8.6.**  $\text{Inv}_{\mathbb{Q}}(\Theta)(\Gamma_+)$  and  $\text{Inv}_{\mathbb{Q}}(\Theta)(\Gamma_0)$  are compact and convex subsets of  $\mathcal{P}(\Gamma)$ .

**Proof.** Since  $\Gamma_+$  and  $\Gamma_0$  are positively invariant compacts,  $\text{Inv}(\Theta)(\Gamma_+)$  and  $\text{Inv}_{\mathbb{Q}}(\Theta)(\Gamma_0)$  are non empty, compact and convex subsets of  $\mathcal{P}(\Gamma)$ . Then, since  $p_1^* \circ \pi_0^*$  is continuous,  $\text{Inv}_{\mathbb{Q}}(\Theta)(\Gamma_+)$  and  $\text{Inv}_{\mathbb{Q}}(\Theta)(\Gamma_0)$  are compacts as closed subsets of  $\mathcal{P}(\Gamma)$ . The convexity of  $\text{Inv}_{\mathbb{Q}}(\Theta)(\Gamma_+)$  and  $\text{Inv}_{\mathbb{Q}}(\Theta)(\Gamma_0)$  is a consequence of the convexity of  $\text{Inv}(\Theta)(\Gamma_+)$  and  $\text{Inv}(\Theta)(\Gamma_0)$ , and the linearity of  $p_1^* \circ \pi_0^*$ . ■

As a consequence of equation (22), we have

**Proposition 8.7.** For every  $\Theta$ -invariant measure  $\tilde{\mu}$  supported on  $\Gamma_+$ ,  $\pi_0^*(\tilde{\mu})$  is  $\Phi$ -invariant.

**Proof.** Let  $\tilde{\mu}$  be a  $\Theta$ -invariant measure supported on  $\Gamma_+$ . Therefore the measure  $\pi_0^*(\tilde{\mu})$  is supported by  $\Omega \times \overline{V}$ . Let  $B \subset \Omega \times \overline{V}$  be a Borel set. We have

$$\begin{aligned} \pi_0^*(\tilde{\mu})(\Phi^{-1}(B)) &= \tilde{\mu}(\pi_0^{-1}(\Phi^{-1}(B))) \\ &= \tilde{\mu}(\pi_0^{-1}(\Phi^{-1}(B) \cap \Omega \times \overline{V})) \\ &= \tilde{\mu}((\Phi|_{\Omega \times \overline{V}} \circ \pi_0)^{-1}(B)) \\ &= \tilde{\mu}((\pi_0 \circ \Theta|_{\Gamma_+})^{-1}(B)) \\ &= \tilde{\mu}(\pi_0^{-1}(B)) \\ &= \pi_0^*(\tilde{\mu})(B). \end{aligned}$$

The second equality is because the support of  $\tilde{\mu}$  is included in  $\Gamma_+$ , and the third is a consequence of the conjugacy (22). ■

**Corollary 8.8.**  $\pi_0^*(\text{Inv}_{\mathbb{Q}}(\Theta)(\Gamma_+))$  is a compact and convex subset of  $\text{Inv}_{\mathbb{Q}}(\Phi)(\Omega \times \overline{V})$ .

**Proof.** Since  $\pi_0^*$  is continuous and linear, Proposition 8.6 implies that  $\pi_0^*(\text{Inv}_{\mathbb{Q}}(\Theta)(\Gamma_+))$  is a compact and convex. Proposition 8.7 implies that  $\pi_0^*(\text{Inv}_{\mathbb{Q}}(\Theta)(\Gamma_+)) \subset \text{Inv}_{\mathbb{Q}}(\Phi)(\Omega \times \overline{V})$ . ■

The map  $\Theta$  on  $\Gamma_+$  can be seen as the extension of the map  $\Phi$  on  $\Omega \times \overline{V}$ . Now, we define the long-term growth rates for the extended dynamics induced by  $\Theta$ .

For each  $i \in \{1, \dots, m\}$ , define the maps  $A_i : \Gamma \rightarrow \mathbf{M}_{n_i}(\mathbb{R})$  by

$$A_i(\gamma) = \begin{cases} A_i(\omega^*, x^*) & \text{if } x_0 = x^* \\ A_i(\omega_0, x_0) & \text{either} \end{cases}$$

As (21), we write

$$(23) \quad A_i^t(\gamma) := A_i(\gamma) \cdots A_i(\Theta^{t-1}(\gamma)).$$

The conjugacy (22) implies that for all  $(\omega, x) \in \Omega \times \overline{V}$  and all  $\gamma \in \pi_0^{-1}(\omega, x)$ , we have

$$(24) \quad A_i^t(\gamma) = A_i^t(\omega, x),$$

for all  $t \geq 0$ .

Then the *long-term growth rates* for the product (24) is

$$r_i(\gamma) := \limsup_{t \rightarrow \infty} \frac{1}{t} \ln \|A_i^t(\gamma)\|,$$

and, for a  $\Theta$ -invariant measure  $\tilde{\mu}$ , the *long-term growth rates* is

$$r_i(\tilde{\mu}) = \int_{\Gamma} r_i(\gamma) d\tilde{\mu}.$$

**Proposition 8.9.** *For all species  $i$ , we have*

- (i)  $r_i(\omega, x) = r_i(\gamma)$ , for all  $(\omega, x) \in \Omega \times \overline{V}$  and for all  $\gamma \in \pi_0^{-1}(\omega, x)$ ,
- (ii) for all  $\tilde{\mu} \in \text{Inv}_{\mathbb{Q}}(\Theta)(\Gamma_+)$ ,  $\pi_0^*(\tilde{\mu}) \in \text{Inv}_{\mathbb{Q}}(\Phi)(\Omega \times \overline{V})$ , and

$$r_i(\tilde{\mu}) = r_i(\pi_0^*(\tilde{\mu})).$$

**Proof.** Assertion (i) is a consequence of equality (24), and assertion (ii) is a consequence of assertion (i) and Corollary 8.8. ■

We can now state an equivalent version of Theorem 8.5 on the space of trajectories  $\Gamma$ .

**Theorem 8.10.** *If one of the following equivalent conditions hold*

- (a)  $r_*(\tilde{\mu}) := \max_{0 \leq i \leq m} r_i(\tilde{\mu}) > 0$  for every probability measure  $\tilde{\mu} \in \text{Inv}_{\mathbb{Q}}(\Theta)(\Gamma_0)$ , or
- (b) there exist positive constants  $p_1, \dots, p_m$  such that

$$\sum_i p_i r_i(\tilde{\mu}) > 0$$

for every ergodic probability measure  $\tilde{\mu} \in \text{Inv}_{\mathbb{Q}}(\Theta)(\Gamma_0)$ , or

- (c) there exist positive constants  $p_1, \dots, p_m$  such that

$$\sum_i p_i r_i(\omega, x) > 0$$

for every  $x \in S_0$  and  $\mathbb{Q}$ -almost all  $\omega \in \Omega$ ,

then for all  $\varepsilon > 0$ , there exists  $\eta > 0$  such that

$$\limsup_{t \rightarrow \infty} \Pi_t(\omega, x)(S_{\eta}) \leq \varepsilon \quad \text{for } \mathbb{Q}\text{-almost all } \omega,$$

whenever  $x \in \mathbb{R}_+^n \setminus S_0$ .

**Remark 8.11.** Condition (c) of Theorem 8.10 and (iii) Theorem 8.5 are equivalent, and the implications from conditions (iii) to (ii) and (ii) to (i) of Theorem 8.5 are direct. The proof of Theorem 8.10 (see section 8.5) shows that (a), (b) and (c) of Theorem 8.10 are equivalent. Finally, condition (i) of Theorem 8.5 implies condition (a) of Theorem 8.10 as a direct consequence of assertion (ii) of Proposition 8.9. Hence, Theorems 8.5 and 8.10 are equivalent.

**8.3. Properties of long-term growth rates.** In this section, we first state Proposition 3.2 of Ruelle [1979b] in its original framework, and extend it to ours. We use our extension to deduce some properties on the long-term growth rates which are crucial for the proof of Theorem 8.10.

**Proposition 8.12** (Ruelle [1979b]). *Let  $\Xi$  be a compact space,  $\Psi : \mathbb{R}_+ \times \Xi \rightarrow \Xi$  be an homeomorphism, and  $\pi : \Xi \times \mathbb{R}^d \rightarrow \Xi$  be the projection map defined by  $\pi(\xi, x) = \xi$ . Consider a continuous map  $T : \Xi \rightarrow \mathbf{M}_d(\mathbb{R})$  and its transpose  $T^*$ . Write*

$$T^t(\xi) = T(\xi) \cdots T(\Psi^{t-1}\xi),$$

and assume that

**A:** for all  $\xi \in \Xi$ ,  $T(\xi)(\mathbb{R}^d) \subset \{0_+\} \cup \text{int } \mathbb{R}_+^d$ .

Then there exist continuous maps  $u, v : \Xi \rightarrow \mathbb{R}_+^d$  with  $\|u(\xi)\| = \|v(\xi)\| = 1$  such that

- (i) the line bundles  $E$  (resp.  $F$ ) spanned by  $u(\cdot)$  (resp.  $v(\cdot)$ ) are such that  $\mathbb{R}^d = E \oplus F^\perp$  where  $b \in F(\xi)^\perp$  if and only if  $\langle \xi, b \rangle = 0$ .
- (ii)  $E$  (resp.  $F$ ) is  $T, \Psi$ -invariant (resp.  $T^*, \Phi^{-1}$ -invariant), i.e.  $E(\Psi(\xi)) = E(\xi)T(\xi)$  and  $F(\Psi(\xi))T^*(\Psi(\xi)) = F(\xi)$ , for all  $\xi \in \Xi$ ;
- (iii) there exist constants  $\alpha < 1$  and  $C > 0$  such that for all  $t \geq 0$ , and  $\xi \in \Xi$ ,

$$\|bT(\xi) \cdots T(\Psi^{t-1}\xi)\| \leq C\alpha^t \|aT(\xi) \cdots T(\Psi^{t-1}\xi)\|,$$

for all unit vectors  $a \in E(\xi), b \in F(\xi)^\perp$ .

Since assumption **H2** does not directly imply assumption **A** for the map  $A_i(\cdot, \cdot)$ , we need to extend Ruelle's proposition to the case where

**A1'**: for all  $\xi \in \Xi$ ,  $T(\xi) \text{int } \mathbb{R}_+^d \subset \text{int } \mathbb{R}_+^d$ , and

**A2'**: there exists  $s \geq 1$  such that, for all  $\xi \in \Xi$ ,  $T(\xi) \cdots T(\Psi^{s-1}\xi)(\mathbb{R}^d) \subset \{0\} \cup \text{int } \mathbb{R}^d$ .

**Proposition 8.13.** *The conclusions of Proposition 8.12 still hold under assumptions **A1'-A2'**.*

**Proof.** Define the continuous map  $T' : \Xi \rightarrow \Xi \times \mathbf{M}_d(\mathbb{R})$  by

$$T'(\xi) = T(\xi) \cdots T(\Psi^{s-1}(\xi)).$$

By assumption (**A2'**),  $T'(\xi)\mathbb{R}_+^d \subset \{0_+\} \cup \text{int } \mathbb{R}_+^d$ . Therefore, Proposition 8.12 applies to the map  $T'$  and to the homeomorphism  $\Psi^s$  which give us maps  $u, v : \Xi \rightarrow \mathbb{R}_+^d$  with  $\|u(\xi)\| = \|v(\xi)\| = 1$ , their respective vector bundles  $E(\cdot), F(\cdot)$ , and some constants  $C, \alpha$  verifying properties (i), (ii), and (iii).

The vector bundles  $E(\cdot), F(\cdot)$  are our candidate bundles for  $T$ . We need only to check properties (ii) and (iii) for the map  $T$  as property (i) is immediate.

We claim that

$$(25) \quad \lim_{t \rightarrow \infty} \frac{xT^t(\Psi^{-t}\xi)}{\|xT^t(\Psi^{-t}\xi)\|} = u(\xi),$$

uniformly on all compact of  $\mathbb{R}_+^d - \{0_+\}$ . Before we prove (25), we show property (ii), i.e.  $E(\cdot)$  is  $T, \Psi$ -invariant, is a consequence (25). Let  $y \in \text{int } \mathbb{R}_+^d - \{0\}$ , and  $\xi \in \Xi$ . Continuity of  $T$  and equality (25) applied to  $y$  imply

$$\begin{aligned} u(\xi)T(\xi) &= \lim_{t \rightarrow \infty} \frac{yT^t(\Psi^{-t}\xi)}{\|yT^t(\Psi^{-t}\xi)\|} T(\xi) \\ &= \lim_{t \rightarrow \infty} \frac{yT(\Psi^{-t}\xi)T^t(\Psi^{-t}(\Psi\xi))}{\|yT^t(\Psi^{-t}\xi)\|} \\ &= u(\Psi\xi) \lim_{t \rightarrow \infty} \frac{\|yT(\Psi^{-t}\xi)T^t(\Psi^{-t}(\Psi\xi))\|}{\|yT^t(\Psi^{-t}\xi)\|}, \end{aligned}$$

where the final line follows from (25) with  $\xi = \Psi\xi$  and  $x = yT(\Psi^{-t}\xi)/\|yT(\Psi^{-t}\xi)\|$  which belongs to the compact  $\{z \in \mathbb{R}_+^d : \|z\| = 1\}$  for all  $t \geq 0$ . This proves property (ii) for  $E$ . The same argument for the transpose  $T'^*$  implies property (ii) for  $F$ . Now we prove (25). Let  $x \in \mathbb{R}_+^d - \{0_+\}$  with  $\|x\| = 1$ . For every  $t \geq 0$ , define  $s_t := t - [\frac{t}{s}]s$  where  $[q]$  is the integer part of  $q$ . We have

$$xT^t(\Psi^{-t}\xi) = xT^{s_t}(\Psi^{-t}\xi)T'^{[\frac{t}{s}]}(\Psi^{-t+s_t}\xi).$$

Since  $s_t \leq s$  for all  $t \geq 0$ , continuity of  $T(\cdot)$ , and assumption **A1'** imply that there is a compact  $H \subset \mathbb{R}_+^d - \{0_+\}$  independent of  $x$  such that  $xT^{s_t}(\Psi^{-t}\xi) \in H$  for all  $t > 0$ . Then, (25) is a consequence of inclusion (3.2) in the proof of Proposition 3.2 in Ruelle [1979b] applied to the map  $T'$ .

It remains to check property (iii): show that there exist  $\alpha', C' > 0$  such that

$$\|bT^t(\xi)\| \leq C'\alpha'^t \|u(\xi)T^t(\xi)\| \text{ for all } t \geq s, \xi \in \Xi, b \in F(\xi)^\perp.$$

We have

$$bT^t(\xi) = bT^{s_t}(\xi)T'^{[\frac{t}{s}]}(\Psi^{s_t}\xi).$$

Since  $F(\cdot)$  is  $T^*$ -invariant,  $bT^{s_t}(\xi) \in F(\Psi^{s_t}\xi)^\perp$  and property (iii) for  $T'$  implies

$$\frac{1}{\|bT^{s_t}(\xi)\|} \|bT^{s_t}(\xi)T'^{[\frac{t}{s}]}(\Psi^{s_t}\xi)\| \leq \frac{C(\alpha'^{\frac{1}{s}})^t}{\|u(\xi)T^{s_t}(\xi)\|} \|u(\xi)T^{s_t}(\xi)T'^{[\frac{t}{s}]}(\Psi^{s_t}\xi)\|.$$

The continuity of  $T(\cdot, \cdot)$  and  $u(\cdot)$ , and assumption **A1'** imply that there exist a constant  $R \geq 0$  such that

$$\frac{\max\{\|wT^k(\xi)\| : \|w\| = 1\}}{\min\{\|u(\xi)T^k(\xi)\| : \xi \in \Xi\}} \leq R,$$

for all  $k \leq s$  and all  $\xi \in \Xi$ . Then property (iii) is verified with  $C' = CR$  and  $\alpha' = \alpha'^{\frac{1}{s}}$ . ■

Proposition 8.13 applies to each continuous map  $A_i : \Gamma \rightarrow \mathbf{M}_{n_i}(\mathbb{R})$ , and to the homeomorphism  $\Theta$  on the compact space  $\Gamma$ . Then, for each of those maps, there exist row vector maps  $u_i(\cdot)$ ,  $v_i(\cdot)$ , their respective vector bundles  $E_i(\cdot)$ ,  $F_i(\cdot)$ , and the constant  $C_i, \alpha_i > 0$  satisfying properties (i), (ii), and (iii) of Proposition 8.13.

For each  $i \in \{1, \dots, m\}$ , define the continuous map  $\zeta_i : \Gamma \rightarrow \mathbb{R}$  by

$$\zeta_i(\gamma) := \ln \|u_i(\gamma)A_i(\gamma)\|.$$

In the rest of this subsection, we deduce from Proposition 8.13 some crucial properties of the invasions rates.

**Proposition 8.14.** *For all  $\gamma \in \Gamma$  and every population  $i$ ,  $r_i(\gamma)$  satisfies the following properties:*

(i)

$$r_i(\gamma) = \limsup_{t \rightarrow \infty} \frac{1}{t} \ln \|v A_i^t(\gamma)\|,$$

for all  $v \in \mathbb{R}_+^{n_i} \setminus \{0\}$ .

(ii)

$$r_i(\gamma) = \limsup_{t \rightarrow \infty} \frac{1}{t} \sum_{s=0}^{t-1} \zeta_i(\Theta^s(\gamma)).$$

The proof is similar to that of proposition 1 in Hofbauer and Schreiber [2010].

**Proof.** Let  $\gamma \in \Gamma$  be fixed. To prove the first part, we start by showing that

$$(26) \quad r_i(\gamma) = \limsup_{t \rightarrow \infty} \frac{1}{t} \ln \|u_i(\gamma) A_i^t(\gamma)\|.$$

Let  $v \in \mathbb{R}^{n_i}$ ,  $v \neq 0$ . Since  $\mathbb{R}^{n_i} = E_i \bigoplus F_i^\perp(\gamma)$ , there exist a constant  $a \in \mathbb{R}$  and a vector  $w \in F_i^\perp$  such that  $v = au_i(\gamma) + w$ . Then, by Proposition 8.13, we have

$$\begin{aligned} \|v A_i^t(\gamma)\| &\leq a \|u_i(\gamma) A_i^t(\gamma)\| + \|w A_i^t(\gamma)\| \\ &\leq \|u_i(\gamma) A_i^t(\gamma)\| (a + C_i \alpha_i^t \|w\|). \end{aligned}$$

Hence,

$$\limsup_{t \rightarrow \infty} \frac{1}{t} \ln \|v A_i^t(\gamma)\| \leq \limsup_{t \rightarrow \infty} \frac{1}{t} \ln \|u_i(\gamma) A_i^t(\gamma)\|$$

for all  $v \in \mathbb{R}^{n_i} \setminus \{0\}$ . Since  $\|A_i^t(\gamma)\| = \sup_{\|v\|=1} \|v A_i^t(\gamma)\|$ , the last inequality implies that

$$r_i(\gamma) \leq \limsup_{t \rightarrow \infty} \frac{1}{t} \ln \|u_i(\gamma) A_i^t(\gamma)\| \leq r_i(\gamma),$$

which proves the equality (26).

Now, we consider positive vector  $v \in \mathbb{R}_+^{n_i} \setminus \{0\}$ . We show that the equality (26) is also satisfied for  $v$ . We write  $v = au_i(\gamma) + w$  with  $a > 0$  and  $w \in F_i^\perp(\gamma)$ . Proposition 8.13 implies

$$\begin{aligned} \|v A_i^t(\gamma)\| &\geq a \|u_i(\gamma) A_i^t(\gamma)\| - \|w A_i^t(\gamma)\| \\ &\geq \|u_i(\gamma) A_i^t(\gamma)\| (a - C_i \alpha_i^t \|w\|). \end{aligned}$$

Since  $a > 0$ ,

$$r_i(\gamma) \geq \limsup_{t \rightarrow \infty} \frac{1}{t} \ln \|v A_i^t(\gamma)\| \geq \limsup_{t \rightarrow \infty} \frac{1}{t} \ln \|u_i(\gamma) A_i^t(\gamma)\| = r_i(\gamma),$$

which completes the proof of assertion (i).

The second assertion results directly from the first assertion and the following equalities:

$$\begin{aligned} \ln \|u_i(\gamma) A_i^{t+1}(\gamma)\| &= \ln \|u_i(\gamma) A_i^t(\gamma) A_i(\Theta^t(\gamma))\| \\ &= \ln \|u_i(\Theta(\gamma)^t) A_i(\Theta^t(\gamma))\| \|u_i(\gamma) A_i^t(\gamma)\| \\ &= \zeta_i(\Theta^t(\gamma)) + \ln \|u_i(\gamma) A_i^t(\gamma)\|. \end{aligned}$$

The second step is a consequence of the invariance of the line bundle  $E_i$ . ■

Recall that  $\Gamma_+ = \pi_0^{-1}(\Omega \times \bar{V})$  and  $\Gamma_0 = \pi_0^{-1}(\Omega \times S_0)$ .

**Remark 8.15.** *Assumption H2 implies that the sets  $\Gamma_0$  and  $\Gamma_+ \setminus \Gamma_0$  are both positively  $\Theta$ -invariant. Therefore every  $\Theta$ -invariant measure  $\tilde{\mu}$  on  $\Gamma_+$  can be written as a convex combination of two  $\Theta$ -invariant measures  $\tilde{\nu}_0$  and  $\tilde{\nu}_1$  such that  $\tilde{\nu}_0(\Gamma_0) = 1$  and  $\tilde{\nu}_1(\Gamma_+ \setminus \Gamma_0) = 1$ .*

**Corollary 8.16.** *For all  $\gamma \in \Gamma_+ \setminus \Gamma_0$ , and every  $i \in \{1, \dots, m\}$ ,*

$$r_i(\gamma) \leq 0.$$

**Proof.** Fix  $i \in \{1, \dots, m\}$ , and  $\gamma \in \Gamma_+ \setminus \Gamma_0$  with  $(\omega, x) := \pi_0(\gamma)$ . By definition of  $\Gamma_+ \setminus \Gamma_0$ ,  $x^i \in \mathbb{R}_+^{n_i}$  and  $x^i \neq 0$ . We have

$$\begin{aligned} x^i A_i^t(\gamma) &= x^i A_i(\gamma) \cdots A_i(\Theta^{t-1}\gamma) \\ &= x^i A_i(\omega, x) \cdots A_i(\Phi^{t-1}(\omega, x)) \\ &= p_2(\Phi^t(\omega, x)), \end{aligned}$$

where the second equality is a consequence of (23), and the third one follows from the definition of the cocycle  $\Phi$ . Assumption **H3'** implies that there exists  $T > 0$  such that  $p_2(\Phi^t(\omega, x))$  belongs to the compact set  $\overline{V}$  for all  $t \geq T$ , which implies that there exists  $R > 0$  such that  $\|x^i A_i^t(\gamma)\| \leq R$  for all  $t \geq T$ . Assertion (i) of Proposition 8.14 applied to  $v = x^i$  concludes the proof. ■

Now we give some properties of the invasion rate with respect to a  $\Theta$ -invariant probability measure.

**Proposition 8.17.** *The invasion rate of each population  $i$  with respect to an  $\Theta$ -invariant measure  $\tilde{\mu}$  satisfies the following property:*

$$r_i(\tilde{\mu}) = \int_{\Gamma} \zeta_i(\gamma) d\tilde{\mu}.$$

**Proof.** This result is a direct consequence of property (ii) of Proposition 8.14 and the Birkhoff's Ergodic Theorem applied to the continuous maps  $\Theta$  and  $\zeta$ . ■

**Proposition 8.18.** *Let  $\tilde{\mu}$  be a  $\Theta$ -invariant measure. If  $\tilde{\mu}$  is supported by  $\Gamma_+ \setminus \Gamma_0$ , then  $r_i(\tilde{\mu}) = 0$  for all  $i \in \{1, \dots, m\}$ .*

**Proof.** Let  $\tilde{\mu}$  be such a probability measure. Fix  $i \in \{1, \dots, m\}$ , and define the set  $\Gamma^{i,\eta} := \{\gamma \in \Gamma_+ : \|p_2(\pi_0(\Theta^t(\gamma)))^i\| > \eta\}$ . By assumption on the measure  $\tilde{\mu}$ , there exists a real number  $\eta^* > 0$  such that  $\tilde{\mu}(\Gamma^{i,\eta}) > 0$  for all  $\eta < \eta^*$ .

The Poincaré recurrence theorem applies to the map  $\Theta$ , and implies that for each  $\eta < \eta^*$ ,

$$(27) \quad \tilde{\mu}(\{\gamma \in \Gamma^{i,\eta} \mid \Theta^t(\gamma) \in \Gamma^{i,\eta} \text{ infinitely often}\}) = 1.$$

Recall that the conjugacy (22) implies that for every  $\gamma \in \Gamma_+$  with  $\pi_0(\gamma) = (\omega, x)$ , we have

$$\begin{aligned} p_2(\pi_0(\Theta^t(\gamma)))^i &= p_2(\Phi^t(\pi_0(\gamma)))^i \\ &= x^i A_i^t(\gamma). \end{aligned}$$

Then, equality (27) means that for  $\tilde{\mu}$ -almost all  $\gamma \in \Gamma^{i,\eta}$  with  $0 < \eta < \eta^*$ ,  $\|x^i A_i^t(\gamma)\| > \eta$  infinitely often. Therefore, Proposition 8.14 (i), applied to  $v = x^i$ , implies that  $r_i(\gamma) = 0$  for  $\tilde{\mu}$ -almost all  $\gamma \in \Gamma^{i,\eta}$ , with  $\eta < \eta^*$ . Hence  $r_i(\gamma) = 0$  for  $\tilde{\mu}$ -almost all  $\gamma \in \bigcup_{n \geq \frac{1}{\eta^*}} \Gamma^{i,1/n} = \Gamma_+ \setminus \Gamma_0$ , which completes the proof. ■

**8.4. Some Lemmas.** Given a trajectory  $\gamma \in \Gamma_+$ , the *empirical occupation measure* of  $\{\Theta^t(\gamma)\}_{t \geq 0}$  is

$$\tilde{\Lambda}_t(\gamma) := \frac{1}{t} \sum_{s=0}^{t-1} \delta_{\Theta^s(\gamma)},$$

and given a point  $(\omega, x) \in \Omega \times \overline{V}$ , the *empirical occupation measure* of  $\{\Phi^t(x, \omega)\}_t$  is

$$\Lambda_t(\omega, x) := \frac{1}{t} \sum_{s=0}^{t-1} \delta_{\Phi^s(\omega, x)}.$$

In this way,  $\Lambda_t(\omega, x)(\Omega \times B) = \Pi_t(\omega, x)(B)$  for every Borel subset  $B \subset \overline{V}$ , and  $x \in \overline{V}$ .

**Lemma 8.19.** *Let  $\gamma \in \Gamma_+$ . Then for all  $t \geq 0$  we have*

$$\pi_0^*(\tilde{\Lambda}_t(\gamma)) = \Lambda_t(\pi_0(\gamma)).$$

**Proof.** Let  $B \subset \Omega \times \overline{V}$  be a Borel set, and  $\gamma \in \Gamma_+$ . Then we have

$$\begin{aligned} \pi_0^*(\tilde{\Lambda}_t(\gamma))(B) &= \tilde{\Lambda}_t(\gamma)(\pi_0^{-1}(B)) \\ &= \frac{1}{t} \sum_{s=0}^{t-1} \delta_{\Theta^s(\gamma)}(\pi_0^{-1}(B)) \\ &= \frac{1}{t} \sum_{s=0}^{t-1} \delta_{\Phi^s(\pi_0(\gamma))}(B) \\ &= \Lambda_t(\pi_0(\gamma))(B). \end{aligned}$$

The third equality is a consequence of the semi conjugacy (22). ■

**Lemma 8.20.** *There exists  $\tilde{\Omega}$  with  $\mathbb{Q}(\tilde{\Omega}) = 1$  such that for all  $\gamma \in \pi_0^{-1}(\tilde{\Omega} \times \overline{V})$ , the set of all weak\* limit point of the family of probability measures  $\{\tilde{\Lambda}_t(\gamma)\}_{t \in \mathbb{N}}$  is a non-empty subset of  $\text{Inv}_{\mathbb{Q}}(\Theta)(\Gamma_+)$ .*

**Proof.** Since  $\mathbb{Q}$  is ergodic (assumption **H4'**), Birkhoff's Ergodic Theorem implies that there exists a subset  $\tilde{\Omega} \subset \Omega$  such that  $\mathbb{Q}(\tilde{\Omega}) = 1$ , and for all  $\omega \in \tilde{\Omega}$ ,

$$(28) \quad \lim_{t \rightarrow \infty} \frac{1}{t} \sum_{s=0}^{t-1} \delta_{\theta^s(\omega)} = \mathbb{Q}$$

(in the weak\* topology). Let  $(\omega, x) \in \tilde{\Omega} \times \overline{V}$  and  $\gamma \in \pi_0^{-1}(\omega, x) \subset \Gamma_+$ . For all  $t \in \mathbb{N}$ , we have

$$(29) \quad p_1^* \circ \pi_0^*(\tilde{\Lambda}_t(\gamma)) = \frac{1}{t} \sum_{s=0}^{t-1} \delta_{\theta^s(\omega)}.$$

Since  $\Gamma_+$  is positively  $\Theta$ -invariant and compact, the set of all weak\* limit point of the family of probability measures  $\{\tilde{\Lambda}_t(\gamma)\}_{t \in \mathbb{N}}$  is a non-empty subset of  $\mathcal{P}(\Gamma_+)$ . Since the maps  $p_1$  and  $\pi_0$  are continuous, equalities (28) and (29) imply that  $p_1^* \circ \pi_0^*(\tilde{\mu}) = \mathbb{Q}$ . Moreover, Theorem 6.9 in Walters [1982] implies that  $\tilde{\mu}$  is  $\Theta$ -invariant. Therefore,  $\tilde{\mu} \in \text{Inv}_{\mathbb{Q}}(\Theta)(\Gamma_+)$ , which concludes the proof. ■

Recall that  $S_\eta = \{x \in S : \|x^i\| \leq \eta \text{ for some } i\}$ , and define the subset  $\Gamma_\eta := \{\gamma \in \Gamma_+ : \pi_0(\gamma) \in \Omega \times S_\eta\}$ .

**Lemma 8.21.** *If condition (a) of Theorem 8.10 is satisfied, then for all  $\varepsilon > 0$  there exists  $\eta^* > 0$  such that*

$$\tilde{\mu}(\Gamma_\eta) < \varepsilon, \quad \forall \eta < \eta^*,$$

for all  $\tilde{\mu} \in \text{Inv}_{\mathbb{Q}}(\Theta)(\Gamma_+ \setminus \Gamma_0)$ .

**Proof.** If false, there exist  $\varepsilon > 0$  and a sequence of measures  $\{\tilde{\mu}_n\}_{n \in \mathbb{N}} \subset \text{Inv}_{\mathbb{Q}}(\Theta)(\Gamma_+ \setminus \Gamma_0)$  such that  $\tilde{\mu}_n(\Gamma_{1/n}) > \varepsilon$  for all  $n \geq 1$ . By Proposition 8.6, let  $\tilde{\mu} \in \text{Inv}_{\mathbb{Q}}(\Theta)(\Gamma_+)$  be a weak\* limit point of the sequence  $\{\tilde{\mu}_n\}_{n \in \mathbb{N}}$ . Proposition 8.18 implies that  $r_*(\tilde{\mu}_n) = 0$  for all  $n \geq 0$ . Proposition 8.17 and weak\* convergence imply that  $0 = \lim_{n \rightarrow \infty} r_i(\tilde{\mu}_n) = r_i(\tilde{\mu})$  for all  $i$ . Hence,  $r_*(\tilde{\mu}) = 0$ . The Portmanteau theorem (see e.g. Theorem 2.1. in Billingsley [1999]) applied to the closed set  $\Gamma_{1/n}$  implies that for all  $n \geq 1$ ,

$$\begin{aligned}\tilde{\mu}(\Gamma_{1/n}) &\geq \liminf_{m \rightarrow \infty} \tilde{\mu}_m(\Gamma_{1/n}) \\ &\geq \liminf_{m \rightarrow \infty} \tilde{\mu}_m(\Gamma_{1/m}) \\ &\geq \varepsilon.\end{aligned}$$

Therefore  $\tilde{\mu}(\Gamma_0) = \tilde{\mu}(\cap_n \Gamma_{1/n}) \geq \varepsilon$ . Remark 8.15 implies there exist  $\alpha > 0$  such that  $\tilde{\mu} = \alpha \tilde{\nu}_0 + (1 - \alpha) \tilde{\nu}_1$  where  $\tilde{\nu}_0, \tilde{\nu}_1$  are  $\Theta$ -invariant probability measures satisfying  $\tilde{\nu}_0(\Gamma_0) = 1$  and  $\tilde{\nu}_1(\Gamma_+ \setminus \Gamma_0) = 1$ . By Proposition 8.18,  $r_i(\tilde{\nu}_1) = 0$  for all  $i \in \{1, \dots, k\}$ . Condition (a) implies that  $r_*(\tilde{\nu}_0) > 0$ , in which case  $0 = r_*(\tilde{\mu}) = \alpha r_*(\tilde{\nu}_0) > 0$  which is a contradiction. ■

**8.5. Proof of Theorem 8.10.** In the first part of the proof, we show that condition (a) implies the conclusion of Theorem 8.10. The second part is devoted to showing the equivalence of conditions (a), (b) and (c).

Let  $\tilde{\Omega} \subset \Omega$  be defined as in Lemma 8.20. Choose  $(\omega', x') \in \tilde{\Omega} \times \mathbb{R}_+^n \setminus S_0$  and  $\gamma \in \pi_0^{-1}(\omega', x') \subset \Gamma_+ \setminus \Gamma_0$ . By definition of the set  $\bar{V}$ , there exists a time  $T \geq 0$  such that  $\Phi^t(\omega', x') \in \Omega \times \bar{V}$ , for all  $t \geq T$ . Since  $\mu$  is a weak\* limit point of the family  $\{\Lambda_t(\Phi^T(\omega', x'))\}_{t \geq 0}$  if and only if it is a weak\* limit point of the family  $\{\Lambda_t(\omega', x')\}_{t \geq 0}$ , we do not loss generality by considering  $\{\Lambda_t(\Phi^T(\omega', x'))\}_t$ . Since  $\Omega \times \bar{V}$  is compact, the set of all weak\* limit points of the family of probability measures  $\{\Lambda_t(\Phi^T(\omega', x'))\}_{t \in \mathbb{N}}$  is a non-empty subset of  $\mathcal{P}(\Omega \times \bar{V})$ . Let  $\mu = \lim_{k \rightarrow \infty} \Lambda_{t_k}(\omega, x)$  be such a weak\* limit point. Since  $\Gamma_+$  is positively  $\Theta$ -invariant and compact, passing to a subsequence if necessary, there exists  $\tilde{\mu} = \lim_{k \rightarrow \infty} \tilde{\Lambda}_{t_k}(\gamma) \in \mathcal{P}(\Gamma_+)$ . By Lemma 8.20,  $\tilde{\mu} \in \text{Inv}_{\mathbb{Q}}(\Theta)(\Gamma_+)$ . Furthermore by Lemma 8.19 and continuity of  $\pi_0$ ,  $\pi_0^*(\tilde{\mu}) = \mu$ . Hence, Proposition 8.17, the continuity of the map  $\zeta$ , and property (ii) of Proposition 8.14, imply the following equalities for all  $i$ :

$$\begin{aligned}r_i(\tilde{\mu}) &= \int_{\Gamma} \zeta(\eta) d\tilde{\mu}(\eta) \\ &= \lim_{k \rightarrow \infty} \frac{1}{t_k} \sum_{s=0}^{t_k-1} \zeta(\Theta^s(\gamma)) \\ &\leq r_i(\gamma).\end{aligned}$$

Hence, by Corollary 8.16,

$$r_i(\tilde{\mu}) \leq 0, \quad \text{for all } i.$$

Remark 8.15 implies there exists  $\alpha \geq 0$  such that  $\tilde{\mu} = \alpha \tilde{\nu}_0 + (1 - \alpha) \tilde{\nu}_1$  where  $\tilde{\nu}_j$  are invariant probability measure satisfying  $\tilde{\nu}_0(\Gamma_0) = 1$  and  $\tilde{\nu}_1(\Gamma_+ \setminus \Gamma_0) = 1$ . By Proposition 8.18,  $r_i(\tilde{\nu}_1) = 0$  for all  $i \in \{1, \dots, k\}$ . Condition (a) implies  $r_*(\tilde{\nu}_0) > 0$ . Therefore  $\alpha$  must be zero, i.e.  $\tilde{\mu}(\Gamma_+ \setminus \Gamma_0) = 1$ . Fix  $\varepsilon > 0$ . By Lemma 8.21 there exists  $\eta^* > 0$  such that

$$\tilde{\mu}(\Gamma_\eta) < \varepsilon, \quad \forall \eta < \eta^*,$$

which implies

$$\mu(\Omega \times S_\eta) < \varepsilon, \quad \forall \eta < \eta^*.$$

Since  $\eta^*$  does not depend on  $\mu$ , we have

$$\limsup_{t \rightarrow \infty} \Lambda_t(\omega', x')(\Omega \times S_\eta) < \varepsilon, \quad \forall \eta < \eta^*,$$

for all  $x' \in \mathbb{R}_+^n \setminus S_0$  and  $\omega' \in \tilde{\Omega}$ , which implies that (1) is stochastically persistent.

Second, we show the equivalence of the conditions (a) and (b). We need the following version of the minimax theorem (see, e.g., Simmons [1998]):

**Theorem 8.22** (Minimax theorem). *Let  $A, B$  be Hausdorff topological vector spaces and let  $\mathcal{L} : A \times B \rightarrow \mathbb{R}$  be a continuous bilinear function. Finally, let  $E$  and  $F$  be nonempty, convex, compact subsets of  $A$  and  $B$ , respectively. Then*

$$\min_{a \in E} \max_{b \in F} \mathcal{L}(a, b) = \max_{b \in F} \min_{a \in E} \mathcal{L}(a, b).$$

We have that

$$\min_{\tilde{\mu}} \max_i r_i(\tilde{\mu}) = \min_{\tilde{\mu}} \max_p \sum_i p_i r_i(\tilde{\mu})$$

where the minimum is taken over  $\tilde{\mu} \in \text{Inv}_{\mathbb{Q}}(\Theta)(\Gamma_0)$  and the maximum over  $p \in \Delta := \{p \in \mathbb{R}_+^m : \sum_i p_i = 1\}$ . Define  $A$  to be the dual space to the space bounded continuous functions from  $\Gamma_0$  to  $\mathbb{R}$  and define  $B = \mathbb{R}^m$ . Let  $E = \Delta$ , and  $D = \text{Inv}_{\mathbb{Q}}(\Theta)(\Gamma_0) \subset A$  which is nonempty, convex and compact by Proposition 8.6. Let  $\mathcal{L} : A \times B \rightarrow \mathbb{R}$  the bilinear function defined by  $\mathcal{L}(\tilde{\mu}, p) := \sum_i p_i r_i(\tilde{\mu})$ . Proposition 8.17 implies that  $\mathcal{L}$  is continuous. With these choices, the Minimax theorem implies that

$$(30) \quad \min_{\tilde{\mu}} \max_i r_i(\tilde{\mu}) = \max_{p \in \Delta} \min_{\tilde{\mu}} \sum_i p_i r_i(\tilde{\mu})$$

where the minimum is taken over  $\tilde{\mu} \in \text{Inv}_{\mathbb{Q}}(\Theta)(\Gamma_0)$ . By the ergodic decomposition theorem, the minimum of the right hand side of (30) is attained at an ergodic probability measure with support in  $\Gamma_0$ . Thus, the equivalence of the conditions is established.

Third, we show the equivalence of condition (b) and (c). As a direct consequence of assertion (i) of Proposition 8.9, condition (c) implies (b). To prove the other direction, let  $\tilde{\Omega} \subset \Omega$  be defined as in the proof of Lemma 8.20. Choose  $(\omega', x') \in \tilde{\Omega} \times S_0$ . By the same arguments as above, there exist  $T > 0$ ,  $\gamma \in \pi_0^{-1}(\Phi^T(\omega', x')) \subset \Gamma_0$  and  $\tilde{\mu} \in \text{Inv}_{\mathbb{Q}}(\Theta)(\Gamma_0)$  such that

$$\begin{aligned} r_i(\tilde{\mu}) &= \int_{\Gamma} \zeta(\eta) d\tilde{\mu}(\eta) \\ &= \lim_{k \rightarrow \infty} \frac{1}{t_k} \sum_{s=0}^{t_k-1} \zeta(\Theta^s(\gamma)) \\ &\leq r_i(\gamma). \end{aligned}$$

Assertion (i) of Proposition 8.9 implies that  $r_i(\gamma) = r_i(\Phi^T(\omega', x'))$ . Since  $\Phi^T(\omega', x')$  is on the same trajectory that  $(\omega', x')$ ,  $r_i(\tilde{\mu}) \leq r_i(\Phi^T(\omega', x')) = r_i(\omega', x')$ . Writing  $\tilde{\mu}$  as a convex combination of ergodic probability measures, condition (b) implies  $\sum_i p_i r_i(\omega', x') > 0$ . ■

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